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CONTENTS

Population Ecology of the Spadefoot Toad, *Scaphiopus h. Holbrookii* (Harlan)

Paul G. Pearson
(Pp. 233-267)

Studies on Population Productivity. I. Three Approaches to the Optimum Yield Problem in Populations of *Tribolium confusum*

Kenneth E. F. Watt
(Pp. 269-290)

Trophic Structure and Productivity of a Windward Coral Reef Community on Eniwetok Atoll

Howard T. Odum and Eugene P. Odum
(Pp. 291-320)

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POPULATION ECOLOGY OF THE SPADEFOOT TOAD, *SCAPHIOPUS H. HOLBROOKI* (HARLAN)

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TABLE OF CONTENTS

	PAGE		PAGE
INTRODUCTION	233	DISPERSAL	248
DESCRIPTION OF SCAPHIOPUS HABITATS	234	POPULATION DENSITY	250
DESCRIPTION OF RESEARCH PLOTS.....	234	Techniques of analysis	250
METHODS OF STUDY	237	Census results	252
TOAD ACTIVITIES	238	NATALITY	254
Underground activities	238	Reproduction	254
Presence or absence of activity	238	Growth	255
Rates of activity	240	Age group distribution	258
Feeding activities	242	SURVIVAL AND DISAPPEARANCE RATES	259
SPATIAL RELATIONSHIPS	243	DISCUSSION	260
Spatial distribution	243	SUMMARY	264
Home range	244	LITERATURE CITED	266

INTRODUCTION

The spadefoot toad of eastern United States (*Scaphiopus h. holbrooki*) has aroused keen interest among biologists since before the middle of the 19th Century. It has received this attention from scientists because of its secretive habits, because of its amazingly sudden appearances in very large breeding groups during periods of heavy rainfall, and because of its interesting embryonic development. Much has been written about the secretive behavior and the sudden but sporadic breeding choruses, and the literature has been well summarized by Wright (1932). This spadefoot breeds only in temporary water, and probably correlated with this larval habitat is its rapid embryonic development, which has been studied in other species by the Trowbridges (1937) and Trowbridge (1941, 1942). Trowbridge (1941) states, "In *Scaphiopus bombifrons*, the rate of development throughout the entire embryonic and larval period is more rapid than that which has been reported for any other amphibian. The cleavages in particular take place with surprising speed: they are among the most rapid cell divisions ever recorded." A study of larvae of *S. holbrooki* was made by Richmond (1947) that opened vistas for further study of the social phenomena in tadpole aggregations.

The spadefoot toad is abundant in Florida, espe-

cially in the upland forests. It spends much of its life in underground burrows from which it emerges during certain nights. This species is not nearly as secretive as reported in the literature and in the Gainesville region it can be observed on a majority of nights of the year. The abundance of this animal, the ease with which it is captured, and an obvious need for further study of its habits make it an ideal animal for a population study.

Discussion of population studies by Allee *et al.* (1949) illustrated a need for field data to support many generalizations and especially a need is seen for observation of terrestrial cold-blooded vertebrates. Stickel (1950) made an extensive study of the home range and population factors of the box turtle while Carpenter (1952) made a comparative study of three garter snake populations. Dice (1952) states: "At the present time thorough and long continued quantitative studies of the rates of increase, rates of mortality, and fluctuations of populations living under natural conditions are very much needed."

A major objective of the present research was to raise by field observation and experimentation the base level of factual information on the spadefoot toad. This population study of an adult, terrestrial amphibian was concerned with its spatial relationships, density, age group distribution, mortality and growth rates, and general surface activities in its natural environment. Discussions of various interrelationships of these factors are presented. Asso-

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ciation between spadefoot activity and a number of environmental factors was examined. Throughout the entire study, and especially in the observation of activity and its relationship to the physical environment, statistical tools were used to help define the relations more precisely.

Many individuals gave generously of helpful suggestions and criticisms, and for this I wish to thank Olive and Coleman J. Goin, Archie Carr, H. T. Odum, R. A. Edwards, and W. L. Jennings. Many have helped physically in construction of field projects and I gratefully acknowledge the help of W. Auffenberg, J. Crenshaw, K. Hansen, W. McLane, B. B. Leavitt, A. Carr, and A. M. Laessle, who also aided in plant identification. Mr. Erdman West helped with the botanical nomenclature and A. B. Grobman and Warren Hansen gave advice on statistical matters, although I take full responsibility for any errors in theory or detail found herein. Doctors A. Carr and J. C. Dickinson kindly offered the use of their respective lands for study and the College of Arts and Sciences gave a fellowship for the summer of 1953. Two persons deserve most special acknowledgment. The late Dr. W. C. Allee guided my academic program, wisely led my research, and gave me inspiration. My wife, Winifred Pearson, has helped in the field study, has given aid and suggestions in writing this report, and has provided financial and moral support.

DESCRIPTION OF SCAPHIOPUS HABITATS

The Gainesville region is on the center of an elongated ridge section of Florida, designated as the Central Highlands topographic division by Cooke (1945). Surface features north of Gainesville include a relatively flat area with elevations of 150 ft. and higher dominated mainly by pine forests. To the south of the city are gently rolling hills between 70 and 130 ft. in elevation with much of the surface about 80 ft. above sea level. A mantle of Pleistocene sands covers some 4000 ft. of sedimentary bedrock, of which most is limestone. These rocks are eroded by subsurface solution producing typical Karst topography of solution lakes, prairies, and sink holes. A number of large level prairies are found south and southwest of Gainesville and most are at about 60 ft. elevation; in this region the mantle is thin enough to permit frequent outcrops of bedrock.

According to Carr (1940) adult *Scaphiopus* is a characteristic element of upland hammocks, is frequently found in high pine woods, and is occasionally seen in rosemary scrub, low and mesophytic hammocks, and palmetto flatwoods. Plant communities somewhat similar to those were described and defined in detail at Welaka, Florida, by Laessle (1942), who used a slightly different habitat nomenclature. In the present study largest toad populations were observed in upland hammocks (xeric hammock, of Laessle, *ibid.*), mesophytic hammocks, and in ecotonal areas at the margins of hardwood forests. Spadefoot toads were also seen in old fields, pastures, and other ruderal

habitats that were areas cleared of one of the major communities mentioned above.

The soils of the major toad habitats are alike in that they are all well drained, they are generally loose and friable, they are derived from surficial sands, and there is no extensive accumulation of organic materials. The xeric and mesophytic hammocks have Kanapaha and Blichten soils. Those of the mesic hammock are generally more moist and darker in color and there is a greater proportion of organic material than in the more leached soils.

The climate of north Florida from April through October is dominated by maritime tropical (mT) air masses from the Caribbean area, and mT air is also present for much of the remaining months. Hot and humid weather is characteristic, with convectional precipitation from June to September accounting for about half of the average annual rainfall of 49 in. During the summer months there is little temperature variation.

From October through April there is usually a continual rhythmic variation between several days of tropical weather and several days of cooler weather resulting from invasion of polar air masses. Thus there is greater temperature fluctuation during these months. Cyclonic rainfall occurs in connection with low pressure systems and frontal weather in advance of polar air movements during these months. The polar air masses have high evaporation rates and if these circulations are situated so that north to north-westerly winds occur in Gainesville, cold and dry weather exists. On the other hand, if these polar masses move further eastward so that wind trajectory is from an easterly direction, they pick up moisture over the Atlantic and bring a moist, raw, but generally not as cold type of weather to Gainesville.

DESCRIPTION OF RESEARCH PLOTS

The present study was started in June, 1951, and was continued through November, 1953. Three plots were selected as sites for population studies, and these areas were chosen with regard to the size of the spadefoot population, plant communities, expected permanency of the habitat, and convenience of travel to the site. The plots will hereafter be referred to and described at plots 1, 2, and 3.

Plot 1. Plot 1 is located about 5 mi. southwest of Gainesville in Range 19 E, Township 110 S, Section 16, and its elevation is 60 ft. This plot was normally studied once each week from July 19, 1951, until September, 1953. However, if the weather was such that toads were inactive, as during cold dry winter periods, these weekly visits to the plot were not regularly made. This plot as originally surveyed measured 200 by 300 ft. with the longer axis paralleling an ecotone between a xeric hammock community and a grass prairie (Fig. 1). A 100-ft. grid system and three 10-ft. grid systems were used and grid lines were numbered and lettered. The intersections of the grid lines were made plainly visible for nocturnal study by the insertion of white stakes at these points.

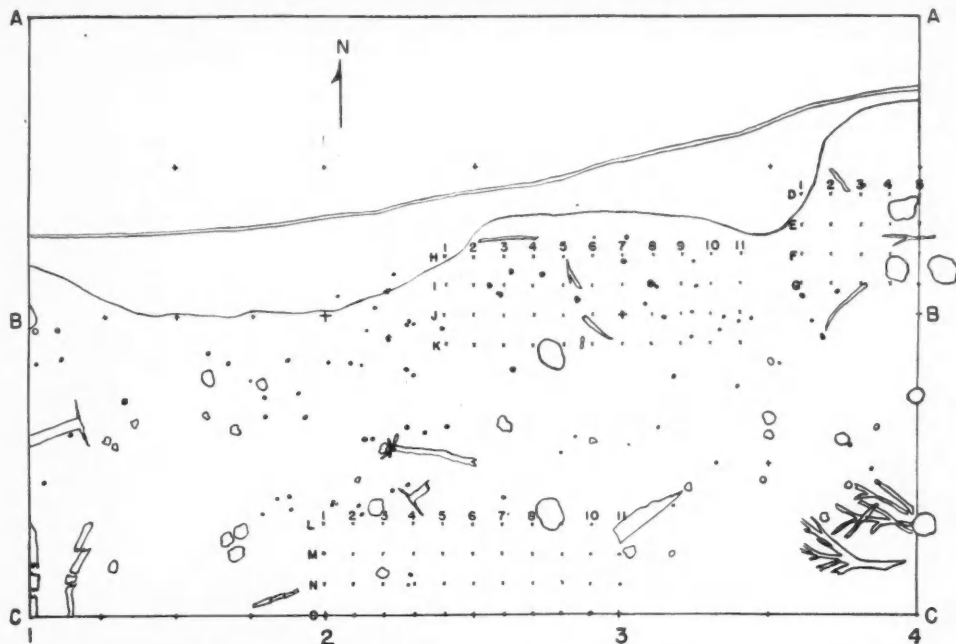


FIG. 1. The crosses show position of grid stakes; live oak trees are indicated by open circles, smaller trees by dots. The letters and numbers designate the grid lines, and the location of fallen logs is also given.

The canopy of the forested portion of this plot was dominated by large live oaks (*Quercus virginiana*) and an occasional sweet gum (*Liquidambar styraciflua*), pignut hickory (*Carya glabra megacarpa*), and Florida maple (*Acer floridanum*). Underneath, especially near the ecotone, were many smaller trees most of which were less than 40 ft. tall. This stratum was composed of American holly (*Ilex opaca*), sweet gum, laurel oak (*Quercus laurifolia*), Florida elm (*Ulmus floridana*), and black gum (*Nyssa sylvatica*). The shrub stratum near lines L-O was sparse and composed of a few French mulberry (*Callicarpa americana*), young laurel oak, sweet gum, and American holly plants. Between lines K and L the plants in this layer were more dense, with laurel oak, American holly, dwarf sumac (*Rhus copallinum*), and French mulberry most abundant. A hawthorn (*Crataegus* sp.), toothache tree (*Zanthoxylum clava-herculis*), and black haw (*Viburnum obovatum*) were of less importance. In the ecotone between lines H and K, young sweet gum, laurel oak saplings and St. Andrew's cross (*Ascyrum hypericoides*) formed the sparse vegetation in the shrub layer of the community. Plant names for trees are according to West and Arnold (1946) and for other vegetation to Small (1933), except where they conflict with the International Code for Nomenclature.

Vines recorded in the plot were poison ivy (*Rhus toxicodendron*), Virginia creeper (*Parthenocissus quinquefolia*), pepper vine (*Ampelopsis arborea*),

trumpet vine (*Bignonia radicans*), and muscadine grape (*Vitis* sp.).

The highest elevations of the plot were along the south border. In this area the dense mat of herbaceous vegetation and vines was dominated by ironweed (*Vernonia gigantea*), yellow jessamine (*Gelsemium sempervirens*), partridge berry (*Mitchella repens*), and violets (*Viola* sp.). Of common occurrence here were two species of panic grass (*Panicum* spp.), elephant's foot (*Elephantopus tomentosus*), bedstraw (*Galium* sp.), creeping cucumber (*Melothria crassifolia*), *Ruellia* sp., *Smilax* sp., spurge nettle (*Jatropha stimulosus*), and woods grass (*Opismenus setarius*).

An ecotone between the hardwood forest and the treeless grass prairie was marked by a gradual decrease in tree size towards the prairie and an abrupt change from a sparse herbaceous vegetation under the canopy to a dense vegetation on the prairie side of the tension zone. In the prairie a dense stand of dogfennel, groundsel tree (*Baccharis halimifolia*) and bagpod (*Glottidium vesicarium*) were dominant. In the low herbaceous level a mat of plants included sensitive plants (*Leptoglottis microphylla*), Florida betony (*Stachys floridana*), sun rose (*Crocanthemum corymbosum*), frog fruits (*Lippia nodiflora*), a fleabane (*Erigeron* sp.), a rush (*Juncus* sp.), sedges (*Rhynchospora* spp. and *Carex* sp.) and grasses (*Panicum* spp. and *Paspalum* spp.). Most of this vegetation was killed in August, 1953, when the entire prairie was inundated for several weeks.

The soils of the higher elevations to the south of the plot have been classified as Kanapaha fine sands. They were generally loose, friable, and well drained. Moving north in the plot, the elevation decreased rapidly about 15 ft. to the prairie where Plummer fine sands occurred. Outcrops of bedrock indicated the margin of the lower prairie which resulted from solution of the limestone bedrock. The soils of the ecotone were intermediate between the above two types. The soils of the entire plot were thin, nowhere being more than 36 in. thick over the bedrock.

Slight water seepage from higher elevations to the ecotone and prairie habitats produced the generally more moist soils of the latter. Tests of soil moisture were made with a Wheatstone bridge circuit and gypsum conductivity blocks placed in the soil at 1 and 3 in. depth at the highest elevation (C 3 in Fig. 1) and in the ecotone. The obvious relationship between soil moisture and rainfall was noted, and the soils of the ecotone were consistently wetter than those of the hammock. In the hammock during dry periods the surface moisture was higher, but after considerable rainfall an overturn in moisture relations resulted in wetter soils at 3 in. than at the surface.

This plot was surveyed with the idea that it would all be utilized in study and that a comparison of the toads in the prairie, in the hammock, and in the ecotone would be made. It was soon apparent that collecting toads in the dense prairie grasses was impracticable. Therefore the work done in the plot was confined to the ecotone and hammock areas. When it was later decided that more precise locations of captures were needed, collection of data was mainly directed to the 3 areas surveyed in a 10-ft. grid system. Throughout the study data were taken from toads in any part of the plot where they were seen, although the most effort was spent in the small grid systems.

In the late spring of 1953, a trap system was built on the east end of this plot. This trap was constructed using two hardware cloth drift fences each 100 ft. long that were placed in a northeast-southwest and a northwest-southeast direction in the shape of a +. Buried lard cans were placed at the inner angles of the fence and smaller traps were buried on either side of each of the extremities of the trap. The trap was placed so that the northwest and southwest extremities of the system were 30 ft. from the east border of the plot. This distance was selected to avoid trapping toads resident in the plot during their normal daily activities. The main object of the trap was to determine the presence or absence, and the rate of dispersal by residents in the plot.

Plot 2. Plot 2 was in the College of Pharmacy drug gardens of the University of Florida campus. Much of these gardens had a park-like appearance with the herbaceous and shrub vegetation removed, and replaced by a lawn and cultivated shrubs. However, in the northwest corner the leaves were allowed to remain on the ground, and the herbaceous vegetation was not lawn-like even though it was occasionally clipped by a power mower. This northwest portion

of the gardens was surveyed into a grid system of lines 10 ft. apart; beginning in the northwest corner of the plot lines A-N were set southward, and lines 1-13 in the eastward direction. This provided a square plot 130 ft. on each side.

The elevation of this plot was lowest in the southwest corner (N-1) and increased about 5 ft. to the north, northeast, and east. In the area between lines 3-13 and B-H, cultivated plants were growing and the arborescent vegetation was scant. Leaf litter was not abundant in this area and it appeared that soil temperatures and soil moisture would vary more in this open unprotected portion than in the remainder of the plot. In the remaining part of the surveyed plot a thick arboreal vegetation was dominated by hickory, sweet gum, and live oak. Loblolly pine (*Pinus taeda*), cedar (*Juniperus silicicola*), black gum, and plum (*Prunus angustifolia*) were present.

Shrub vegetation was absent. The rather sparse herbaceous component comprised primarily panic grasses (*Panicum* spp.), partridge berry, violets, and elephant's foot. Other herbs were a bedstraw (*Galium pilosum*), wild potato (*Ipomea pandurata*), Virginia creeper, poison ivy, and *Ruellia* sp.

Research was begun here in August, 1951, and was continued through September, 1953. From December 1, 1951, through March 23, 1953, an effort was made to visit the plot about 5 nights weekly. The visits were made under all types of weather even though on many occasions it seemed obvious that no toads would be active. The time of the visits was scattered at random between the hours of 6-11 p.m.

The purpose of the nightly field work was to obtain data on the factors influencing activity rates and to gather data on burrow habits and home ranges. The nightly work was limited to 15 min. duration, which was the length of time needed to cover the plot adequately. If in this length of time, no toads were observed, it was assumed that no activity existed for that particular set of conditions.

Plot 3. In the spring of 1952, a semi-controlled population density experiment in fenced areas was established. The location of such an experiment not only needed to be relatively permanent and within easy travelling distance, but it needed to be one where the equipment was safe and where cattle would not trample the fence. An area with these attributes and with a plant community similar to that of plots 1 and 2 was found at the Carr's farm west of Micanopy, Alachua County, Florida at an elevation of 110 ft.

Preliminary experiments showed that a hardware cloth fence of $\frac{3}{8}$ in. mesh would retain the toads if it were buried 12 in. below and reached 10 in. above the soil surface. On top of the vertical fence a horizontal strip 5 in. wide was secured. (Fig. 2.) Five circular enclosures were made with such a fence; each pen having a perimeter of 100 ft., a radius of about 15 ft., and enclosing a forest floor of 796 sq. ft. All of the toads resident in the pens were removed in late May and early June and the toads of a particular size group were introduced in late June, 1952. Three levels of population density were established: 10

toads were put in each of two pens (3 and 5 of Fig. 2), 20 toads were introduced into each of two pens (2 and 4), and in the fifth pen, 40 toads were placed (1).

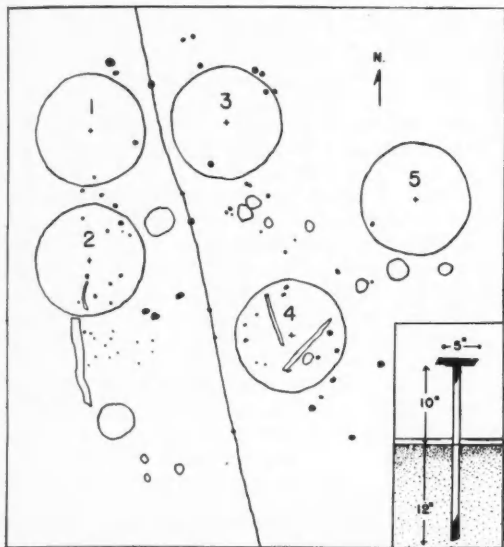


FIG. 2. A map of the five fenced enclosures located on the Carr residence near Micanopy. Open circles designate oak trees while solid dots denote other trees.

In the experimental areas the toads were usually found just inside the fence. This fence also served to collect arthropods, some amphibians (*Bufo terrestris*, *Rana sphenoccephala*, *Rana catesbeiana*), reptiles (*Sceloporus undulatus*, *Thamnophis sirtalis*), and mammals (*Reithrodontomys humulis*, *Peromyscus gossypinus* and *P. nuttalli*). It acted as a barrier for movements by many organisms and the area along the fence was optimal for food capture.

The arborescent vegetation around these plots was dominated by large live oaks, sweet gum, and loblolly pine, while a dense lower layer of smaller trees was dominated by ironwood (*Carpinus caroliniana*), American holly, pignut hickory, black gum, water oak (*Quercus nigra*) and hercules club (*Aralia spinosa*).

The shrub vegetation varied from one pen to another. In pens 2 and 4 no shrub vegetation was present, while in the other three, French mulberry and saplings of laurel oak, sweet gum, and pignut hickory were present in very limited amount. The plots were located in areas of sparse shrub stratum vegetation that were surrounded by dense vegetation composed mostly of wax myrtle (*Myrica cerifera*), laurel oak, live oak, water oak, dwarf sumac, French mulberry, and pignut hickory.

The herbaceous vegetation was scant in pens 3 and 4, in the eastern two thirds of pen 2, and in the eastern third of pen 1. The amount of herbaceous vegetation varied directly with the amount of light;

therefore, with the very dense cover of small trees in pen 3 and in pen 4 the herbs were most sparse. These herbs were elephant's foot, partridge berry, Virginia creeper, pepper vine, *Ruellia* sp., *Panicum* sp., a sedge (*Scleria triglomerata*), bedstraw (*Galium pilosum*), and woods grass.

In pen 5, the west third of pen 2, and the west two-thirds of pen 1, more light reached the floor and a dense carpet of herbs was present. In these areas a ragweed (*Ambrosia* sp.), woods grass, fireweed (*Erechtites hieracifolia*), yellow jessamine, bedstraw, wild potato, a spiderwort (*Tradescantia* sp.) and a smartweed (*Polygonum* sp.) were recorded.

The highest elevations of the area were on the north of pens 1, 3, and 5 with decreases to the south. Pen 4 was at the lowest elevation. The soil of pens 1, 2, and 3 was a Kanapaha fine sand, while in pens 4 and 5 Blichten fine sand occurred. In this area the Kanapaha sands were better drained and generally drier than the Blichten sands.

METHODS OF STUDY

Spadefoot toads do not move rapidly and are easily captured when they are above the soil surface. They are readily seen by the beam of a six volt headlight at distances of 30 to 50 ft. The eyes of the toad reflect a characteristically constant dull red color.

Each animal was marked by removing toes with scissors at the joint between the second and third phalanx. The toes were numbered from right to left on each foot with the left front, right front, left rear, and right rear feet representing, respectively, the elements of a four digit number, i.e. #1111 would have one toe cut on the right side of each foot. In most cases only one toe on each foot was removed.

The greatest head width was measured with vernier calipers to the nearest tenth of a mm. The total length was recorded to the nearest millimeter by holding the snout firmly on a ruler, fastened to a clip board, and by applying steady, gentle pressure to flatten the toad. The sex of the adult male was determined by the presence of dark epidermal pads on the front medial digit whereas most adult females were identified by observable eggs seen through the body wall. The sex of young individuals was not determined. The location of the toad capture and any data concerning the toad's burrow were recorded relative to the particular grid system. All of the above data and any other general observations at capture time were written on a McBee KeySort card (type Ks371N) that measured $3\frac{1}{4} \times 7\frac{1}{2}$ in.

The exact time of capture was not reported, but only the hour of capture. For example, if observation began at 8 p.m. and continued for an hour, all captures were grouped together and recorded as 8 p.m. captures. If field work continued beyond 9 p.m., all of the subsequent hours' captures were listed at that hour.

Measurement of the weather was made at the beginning of the night's work, and at each hour on the hour afterward. The temperature, relative humidity, vapor-pressure deficit, wind movement, and cloud

cover data were added in the laboratory to each of the KeySort cards representing toad captures for the particular unit of time.

Observations of the temperature and humidity were made as nearly as possible in the 3 in. above the soil surface. Several instruments were utilized for this and it is believed that each was an improvement over the earlier ones used by me for measuring the microclimate. In July and August, 1951, wet and dry bulb temperatures were taken with an "egg beater" type psychrometer. This instrument has two thermometers mounted on an egg beater mechanism. From September, 1951, through January, 1952, these data were taken with a standard aspiration psychrometer manufactured by the Friez Instrument Division of the Bendix Aviation Corporation. This instrument was modified by replacing the slower acting standard thermometers supplied with the instrument with quick reading rectal thermometers. The modified instrument was used from February, 1952, through October, 1952. Then an instrument using two Western Electric thermistors and a Wheatstone bridge circuit to measure changes in electrical resistance of the thermistors as the temperature changes was used. This gave sensitive and satisfactory recordings of the microclimate. A similar instrument is described by Platt & Wolf (1950).

No suitable instrument was available to measure small wind velocities under the forest canopy and only general observations were made on wind movements. Records of general cloud cover, rainfall, air mass characteristics, and soil moisture were made.

TOAD ACTIVITIES

UNDERGROUND ACTIVITIES

The spadefoot toad spends much of its lifetime in a burrow measuring from $\frac{3}{4}$ to $1\frac{1}{4}$ in. in diameter and from 2-12 or more inches in depth. The majority of toads was found at depths of less than 8 in. The depth of burrows was given for *S. holbrooki* by Holbrook (1842) as about 6 in., while Ball (1936) found individuals as deep as 2.1 m. Bragg (1944) observed that a direct correlation was exhibited by *S. bombifrons* between depth of burrow and soil moisture. The burrow is usually filled with loose soil and sometimes it can be distinguished only as a tube of loose sand, contrasted to the harder packed earth surrounding it. When leaving the burrow, the animal turns spirally and gradually moves to the surface. Occasionally toads are observed in their burrows below the ground level with a small aperture extending through the soil to the atmosphere. When spadefoots are out of their burrow, a distinct opening can be observed. Upon return, they back into the burrow orifice and disappear from sight by digging with the hind legs.

Each individual had a particular burrow or burrows that it used for considerable periods of time, emerging nocturnally to feed. There was no evidence that more than one toad ever occupied a single burrow. The duration of time that they spend underground without leaving the burrow was checked in plot 2. Finely ground chalk dust was spread on the

surface over the burrow entrance and surrounding soil, with the toad in its burrow, so that subsequent emergence could be detected. If a toad had emerged and reentered its hole in the interval between field trips the chalk was mixed with soil and showed a darker area in the middle of the pure white chalk around the entrance. If the chalk over a burrow remained undisturbed it gave evidence that it had not emerged.

Burrows of 18 individuals in plot 2 were treated in this manner. The duration of time individual burrows were studied varied from 5 to 332 nights. For this study, a toad-night was defined as the record for one individual per night during the duration of study. When three nights elapsed between field trips and an individual's burrow indicated that he had emerged, one toad-night of activity and two of uncertainty were recorded, since emergence on two of the nights was unknown. A total of 2,264 toad-nights was recorded on which activity was unknown or uncertain on 947. Of the remaining 1,317 toad-nights, 1,124 were those when toads definitely did not emerge, while they were active on 193. The toads were active 8% and definitely underground on 58%, and conditions were questionable on 34% of the toad-nights. It is believed that most of this 34% would fall in the inactive category if complete data had been obtained.

If a toad was active on 8% of nights it would emerge from its burrow 29 nights annually. In Table 1 are given records of individuals whose burrows were studied for more than 150 nights. These indicate that emergence on 8% of the nights on a long-term basis is probably the correct order of magnitude.

TABLE 1. Observational data on burrows of several individual toads in plot 2.

Duration of Observation	Number Nights Active	Number Nights per Annum
162.....	16	36
247.....	21	31
278.....	9	15
306.....	23	27
321.....	19	22
332.....	28	31

The length of time individuals remained definitely underground averaged 9.45 days while the median observation was 4.85 days. The extreme record was of 104 days' duration. After activity on June 6, 1951, a female was inactive for 96 days. She emerged one night and was inactive for 11 days, active one night, inactive for 16, active the night of October 13, 1951, and was then inactive for 104 days until emergence on February 20, 1952.

PRESENCE OR ABSENCE OF ACTIVITY

When dates of toad emergence were plotted, the greater number of emergences occurred in the spring and fall, and less in the other seasons. The association between nights of emergence and spring and fall seasons was tested using a four-fold chi square test,

and a significant association existed between emergence and the months of March, April, May, and September, October, and November with a probability of less than 0.01 that the association could be attributed to chance factors alone ($X^2 = 55$). For statistical techniques employed throughout this research reference should be made to standard texts as Simpson & Roe (1939) and Snedecor (1946).

Air temperatures may have contributed to this association with the seasons since they were less extreme during spring and fall. An association between toad-nights of emergence and maximum-minimum daily temperatures that were between 50° and 90° F. was disclosed by a four-fold chi square test ($X^2 = 11$, $P < 0.01$). This means that toads were more apt to be active on nights when the daily maximum-minimum temperature was within this temperature range.

Rainfall was apparently another factor of importance in determining emergence. Independence was tested between the number of toad-nights of emergence (tallied by months) and categories of either more or less than the average monthly rainfall. The results indicate a strong association between nights of emergence and months of more than average rainfall ($X^2 = 40$, $P < 0.01$).

Factors effecting emergence were also examined by measuring environmental factors and comparing these with presence or absence of activity. This was done in plot 2 from December, 1951, through March, 1953, and it was calculated that the temperature of nights showing mean activity was 69.01° F; three standard deviations of toad activity each side of the mean gave the theoretical range of from 48.67° to 89.35° F. Temperatures were recorded on the ground surface and the observed temperature range of activity was 50° to 84° F (Fig. 3).

It was illustrated that rainfall affected activity when the number of nights of toad activity (and no activity) were tallied by weeks and tested for independence with weeks of some recorded rainfall as contrasted with those of no rainfall. A definite association is seen (Table 2) between number of nights of activity and weeks with recorded rainfall.

Since the spadefoot toad has a moist pervious skin it would be more apt to be active on nights when atmospheric moisture is high. The rate of drying that an animal encounters can be closely approximated by use of vapor pressure deficit, as Kucera (1953) showed the correlation of evaporation rate to the vapor pressure deficit exceeded 70%. This deficit in the present study expresses in inches of mercury the difference between saturation vapor pressure and the actual vapor pressure at a given temperature.

Relative humidity and vapor pressure deficit were determined during each nightly visit. The nights were divided into two categories, those with relative humidities 79% and lower and those 80% and higher, and a chi square test showed an association existed between nights of observable activity and nights with 80+% humidity (Table 2). This same procedure using categories of nights with a vapor pressure deficit 0.159 in. mercury and less, and 0.160 in. and

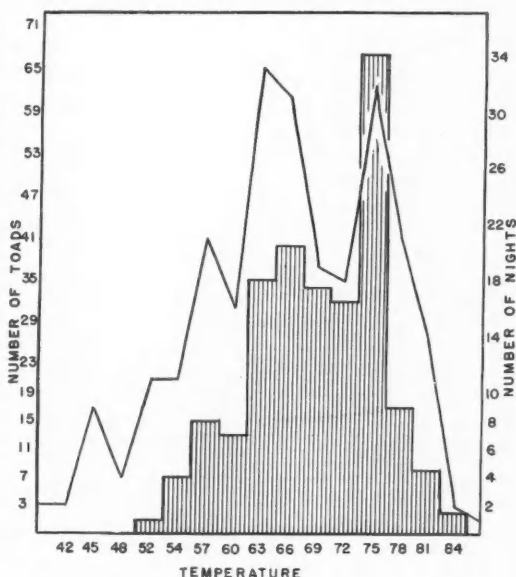


FIG. 3. The histogram illustrates the number of toads caught in Plot 2 for each of the temperature categories; the line represents the number of nights of field work at the various temperatures.

greater showed independence between the lower deficits and nights of activity (Table 2).

It is conceivable that even though association is shown between activity and a factor, temperature for example, the temperature may in turn be associated with rainfall, and the important connection is between activity and rainfall. Therefore several of the factors may be combined and studied by testing association with general weather types. It was noted that polar air masses reaching Gainesville bring either cold-dry, or cold-wet weather depending on their location and the resulting Gainesville wind direction. Maritime tropical weather is usually warm and moist, and frontal and cyclonic weather is connected with much of the rainfall from October through May of each year. The air mass category to which the weather of any particular night belonged was determined by the author from general observations and by use of the daily weather maps published in the Tampa Tribune.

An association was found to exist between nights of activity and cold-wet as contrasted to cold-dry types of weather (Table 3). Since both were cold, significance was attached to the moisture difference. When extremes of both temperature and air moisture were studied using warm-moist contrasted with cold-dry polar weather, a very significant connection was shown (Table 3) between nights of recorded activity and the warm-moist weather. Since the factors of temperature and air moisture were involved, a chi square test of activity contrasting all warm weather and all polar air masses was made to test association between the warm ones and nights of activity, and dependence was shown between these factors (Table

TABLE 2. Chi square tests for association between nights of activity and some climatic factors.

WEEKLY RAINFALL			
	Not Active	Active	Total
Rain	30	58	88
No Rain	94	58	152
Total	124	116	240

$X^2=17$ $P.<0.01$

RELATIVE HUMIDITY			
	Not Active	Active	Total
Less than 79% ..	68	22	90
More than 80% ..	61	103	164
Total	129	125	254

$X^2=34$ $P.<0.01$

VAPOR PRESSURE DEFICIT			
	Not Active	Active	Total
0.159-	37	27	64
0.160+	92	98	190
Total	129	125	254

$X^2=1.7$ $P.=0.20$

3). Comparing all moist air and all dry types in this table, it appears that nights of activity were associated with nights of high air moisture.

RATES OF ACTIVITY

In the foregoing analyses all field trips were classified into categories of nights when toads were or were not active with no mention of rates. Rate of activity as used here is simply the number of individuals captured per 15 min. nightly field trips in plot 2, or number of toads captured per hour in plot 1.

Data are given in Fig. 4 on time of activity in plot 1. Both of the all-night records for number of captures reached a peak after sundown. A smaller peak occurred immediately before sunrise with an intervening low in activity in the early a.m. hours. The two nights differ as a result of the difference in length of summer and winter days. It is notable that in the graph representing average activity rate for the entire study during all seasons, the largest number of captures occurred very early in the evening with a decline in early morning that preceded the second peak before sunrise.

Correlation between activity rate and temperature is shown in Fig. 3 with a peak rate near the mean of 69° F and minimal activity near the extremes of 50° and 84° F. The data presented above that illus-

TABLE 3. Tests for association between nights of recorded activity and various general weather types.

	Not Active	Active	Total
Cold Wet	30	10	40
Cold Dry	38	0	38
Total	68	10	78

$X^2=8.8$ $P.<0.01$

	Not Active	Active	Total
All Cold	68	10	78
All Warm	17	62	79
Total	85	72	158

$X^2=65.9$ $P.<0.01$

	Not Active	Active	Total
Warm Wet	17	62	79
Cold Dry	38	0	38
Total	55	62	117

$X^2=56$ $P.<0.01$

	Not Active	Active	Total
All Wet	52	94	146
All Dry	38	0	38
Total	90	94	184

$X^2=47$ $P.<0.01$

trated an association between non-emergence from burrows and the winter and summer season might indicate (1) that the toads respond to a cyclic, seasonal phenomena and in that sense hibernate during the winter and/or aestivate during the summer, or (2) there are more days of sub-minimal temperature in the winter and summer than in the other seasons. If the first hypothesis is true, the frequency distributions of toads caught per unit time under comparable environments would be statistically different, i.e. significantly heterogeneous. If the second hypothesis were correct, the activity frequencies would not differ significantly from homogeneity.

For this test categories of warm winter nights, cool summer nights, and spring and fall nights were arbitrarily designated after studying annual temperature variations. Warm winter nights were those when the daily maximum exceeded 70° F from December through February. Cool summer nights were those when the temperature maxima did not exceed 90° F from May through September. The activity rate distributions of March and April when the temperature maxima-minima were between 50 and 90° F were

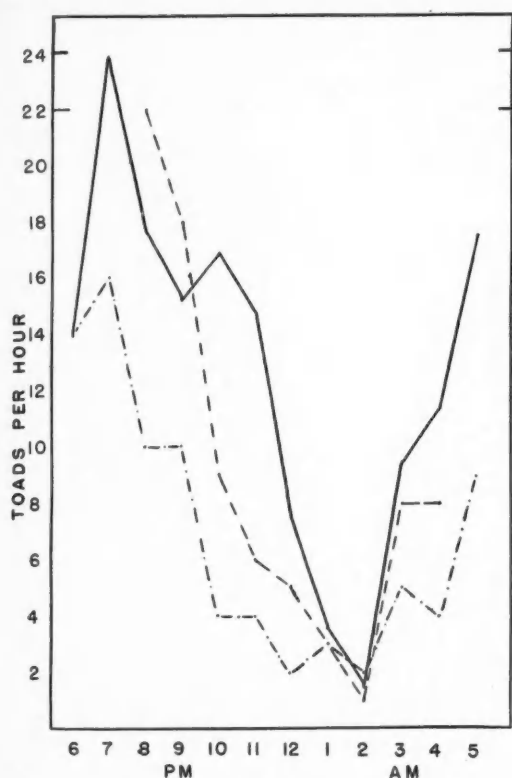


FIG. 4. Plot 1 data on time of activity given here are (1) dots and dashes are for the night of December 30, 1951, (2) dashes equal night of June 14, 1952, and (3) the solid line represents the average for all data.

statistically the same as those of the same temperature range from October and November, so the fall and spring months data were combined. The data of the three categories are given in Table 4.

TABLE 4. Frequency distribution of toads captured per 15 minutes in plot 2.

Number Toads per 15 Min.	Warm Winter Nights	Cool Summer Nights	Average Spring, Fall Nights
0.....	21	10	26
1.....	10	6	10
2.....	14	5	11
3.....	8	2	7
4.....	2	1	7
5+.....	1	3	4

A chi square test for homogeneity in distribution between the warm winter and the cool summer nights showed that the data from the two categories could have been drawn from the same population ($X^2 = 4.3$, 5 d.f., $P = 0.50$). Similarly, tests between the combined winter-summer data and that from the spring and fall months illustrated no statistically sig-

nificant deviation from homogeneity of distribution ($X^2 = 3.9$, 5 d.f., $P = 0.70$). There is no evidence from these data and in this particular test that toads either hibernate or aestivate in the seasonal, cyclical sense; rather the indications are that seasonal differences in activity are more a function of the number of suitable toad-activity nights occurring in the various seasons.

The relationship of temperature and humidity with activity were checked by erecting temperature categories of 53-64, 65-73, and 74-82° F, and relative humidity groups of 89-99, 77-88, and less than 77%, and by plotting mean activity rates. The lowest average rate was 5.5 toads per hour in the 53-64° F and less than 77% relative humidity category, while the highest was 20.8 in the 53-64° F and 89-99% humidity class. Under each of the temperature ranges with an increase in humidity, there followed an increase in mean activity rate, and in general the middle temperature range had higher mean rates within any humidity class. One exception was in the high humidity class where the average activity was 20.8 for the 53-64° F class and only 20 in the 65-73° F category.

The effect of air moisture categories on mean activity rates can be seen in Table 5. A statistically significant difference existed between mean rates under contrasted high and low humidities in plots 1 and 2, as shown by the high *t*. values. Differences between mean activity under the two groups of pressure deficit were significant at the 5% level. A highly significant difference was not shown between means of the two pressure categories, but a reliable difference did occur between the ranges of activity rates in the two categories. A test for real differences between the standard deviations under high and low vapor pressure deficit yielded a *t*. value of 3.6 ($P < 0.01$). The maximum number of toads per hour under low deficits in plot 1 was 55 while it was 37 under high deficits. Under low vapor pressure deficits there was greater variation in the number of captures per unit time than under the drier conditions.

A direct correlation was indicated between activity rate and amount of daily rainfall. In this calculation only those field trips were considered when rainfall was recorded for the day and when toads were active. A significant positive correlation coefficient of 0.31 existed for plot 1 data ($t = 3.2$, $P < 0.01$), and of 0.37 for those from plot 2 ($t = 3.2$, $P < 0.01$). It is concluded that on days of recorded rainfall and activity, the greater the amount of rainfall the higher the activity rate.

The highest rate of activity in plot 1 occurred during frontal weather; (20.1 ± 2.93 average toads per hr.) with the rate decreasing respectively under warm-moist (mT, 15.87 ± 1.01), cold-wet (polar with north-east winds, 14.75 ± 2.44), and cold-dry (polar with northwesterly winds, no activity), weather. The mT weather was further subdivided into mT-wet (17.8 ± 1.10) and mT-dry (9.44 ± 1.52) categories according to the presence or absence of rainfall and moist

TABLE 5. Tests for statistical significance of difference between mean activity of air moisture categories.

Relative Humidity	Mean Activity, Standard Error	Standard Deviation	N.	Significance
Plot 1				
79%—...	11.43 ± 1.65	7.56	21	t = 2.88
80%+...	18.10 ± 0.73	10.31	198	P = 0.01
Plot 2				
79%—...	0.467 ± 0.10	0.945	90	t = 5.77
80%+...	1.494 ± 0.12	1.54	164	P = 0.01
Vapor Pressure Deficit				
Plot 1				
0.160+...	16.02 ± 0.79	8.66	119	t = 2.00
0.159—...	18.87 ± 1.26	12.33	96	P = 0.05
Plot 2				
0.160+...	0.75 ± 0.13	1.04	64	t = 2.44
0.159—...	1.26 ± 0.11	1.54	190	P = 0.05

or dry soils. Even though the atmospheric humidity may have been high, if the soils were quite dry and little rainfall had been recorded, the toad activity was restricted. These activity means for weather types were tested for significant differences and a highly significant difference ($P < 0.01$) existed between means of frontal and mT-dry ($t = 5.0$) and between mT-dry and mT-wet weather ($t = 3.9$). A significant ($P = 0.05$) difference was calculated for the means of wet polar and frontal weather ($t = 2.0$), and between frontal and mT air ($t = 2.1$). All other comparisons of means failed to show statistical significance.

FEEDING ACTIVITIES

A major function of the toad's surface activities is the capture of food. Starting about two hours after sundown and following heavy rainfall in each of four seasons, collections were made in habitats near but no closer than 1000 ft. to plot 1. Stomach contents comprised insects, arachnids, and myriopods. The number of recognizable individuals was tallied (Table 6) and the animal remains were then dried and weighed. By frequency of occurrence, Coleoptera were most abundant with Hymenoptera, Orthoptera, and Arachnida of decreasing importance in the order given. When the dried weight of all collections was pooled, the Coleoptera composed the greatest weight with Orthoptera, Hymenoptera, and Myriopoda decreasing in that order. The increased percentage composition of Coleoptera when weight was considered resulted from larger sized individuals and heavier chitinous elytra, whereas the small bodies of the ants reduced their relative importance.

Considerable variation existed from one collection to the other. From the standpoint of frequency of occurrence, a taxonomic group may have been most abundant during one month whereas the group may have had the least representation during this same month if total dried weight was considered. For example for the Orthoptera (Table 6), the month of least percentage was October, whereas when weight was considered the month of greatest percentage com-

position was also October. The explanation may be that earlier in the year there were many individuals of small size, but that by October although the body size was much larger, the population density had been considerably reduced. A great deal of variation existed in these small samples, and no general conclusions as to seasonal variation were drawn.

TABLE 6. Percentage frequency of occurrence in stomachs of the spadefoot toad.

Date...	Jan. 19	June 8	Aug. 18	Oct. 1	Total
No. of Stomachs...	26	25	22	26	
Orthoptera.....	11	16	12	8	-12
Hemiptera.....	4	—	3	2	2
Homoptera.....	—	4	—	1	1
Lepidoptera.....	3	4	10	2	4
Coleoptera.....	38	33	37	44	39
Hymenoptera.....	25	21	23	34	27
Arachnida.....	12	19	5	4	9
Myriapoda.....	7	3	10	5	6

The capture of prey occurred on the ground surface and generally with the toad out of its burrow. However, toads were observed sitting in the burrow mouth and not protruding above the level of the leaf cover. These observations were made when the environment was near the minimum for toad activity. One such observation in plot 2 on December 5, 1951, was at a temperature of 59° F and a relative humidity of 89%. It seemed reasonable to think that the more favorable the environmental conditions, the further from the burrow an individual toad might move in search of food. It is assumed that the further a toad moves from the burrow, the greater the likelihood of mortality. It seemed important, therefore, to study the relationships of various environmental factors with the distances of movement from a burrow.

The majority of discrete observations recording distance of movement from a burrow were on toads within several feet of the burrow (Table 7). The frequency distribution did not follow a normal curve, and there was strong evidence ($P < 0.01$) that these arrays did not conform to a Poisson distribution, although they were more nearly Poisson than normal. Since the tools for testing significance of difference between populations are based on either normal or Poisson distributions, and could not be used, a chi square test for independence was applied in the study. The difference observed between recorded movements in plots 1 and 2 was real. Although significance of difference in means could not be calculated, the data were divided into cohorts of 5 or less and 6 or more feet and tested by chi square for association with the two plots. A significant association was shown between the greater distances and plot 2 ($P < 0.01$). Since the toad density in plot 1 was higher, this movement difference between plots may be a density effect. The influence of several factors was tested for their relationship to distance of movement. They were:

A. *Sex*. The data from plots 1 and 2 were in-

TABLE 7. Distances of movement during feeding activities measured in feet from a burrow that the given individual was known to occupy.

Distance Movement	Plot 1	Plot 2	Plot 3		
			Pen 1	Pens 2, 4	Pens 3, 5
0-2.....	520	99	65	99	47
3-5.....	167	25	31	45	23
6-8.....	99	21	13	10	25
9-11.....	54	23	9	18	8
12-14.....	16	9	5	1	2
15-17.....	15	10	1	—	3
18-20.....	11	8	1	2	—
21-23.....	3	4	..	1	1
24-26.....	2	4	..	1	..
27-29.....	1	1	..	2	..
30-32.....	1	3
33-35.....	..	—
36+.....	..	2
Total.....	889	209	125	179	109
Mean.....	3.66	6.64	2.76	2.82	3.50

spected to learn if individuals of one sex tended to move further than the other. The average movement in plot 1 for males was 3.69 ft. and for females 3.64 ft. The data for the two sexes were placed in categories of (1) 2 ft. and less, (2) 3-5 ft., (3) 6-14 ft., and (4) 15 ft. and greater, and a X^2 test for independence was made that gave a non-significant value of 0.90. No association existed between movement and sex.

B. Head Width. Using data from plot 1 where both head width and distance of movement were recorded, an association was shown to exist between the two factors. A X^2 test with size categories of 16 mm and less, 17-19 mm, and 20 mm and greater and with distance categories of 0-2 ft., 3-5 ft., and 6+ ft. was designed that revealed a tendency for the smaller toads to be taken at greater distances than would be expected if no correlation existed between body size and movement ($X^2 = 15$, $P = 0.01$).

C. Habitat. The data from plot 1 were separated into those from the ecotone and those from the hammock. The average distance moved in the hammock, 3.07 ft., was less than that in the ecotone, 4.11 ft. Testing the distributions for independence between habitat and distance moved, a significant ($P = 0.01$) association was shown between the ecotone and distances greater than three feet.

D. Population Density. Movement distances were compared under high densities (pen 1), medium densities (pens 2, 4), and low densities (pens 3, 5) from plot 3 (Table 7). The pen with the highest density had the lowest mean movement distance while it increased as the density decreased in the other two levels. The distance data were separated into categories of less than 5 and 6 ft. or more, and independence was tested between them and the three population levels. Independence was shown between distances and the high and middle densities. However, when the middle and low population levels were

tested association was found between the low density and greater movement distances ($X^2 = 4.37$, $P = 0.05$), and the same general relationship held when the highest and lowest levels were compared ($X^2 = 4.5$, $P < 0.05$). Hence, population density was one factor affecting the amount of movement from a known burrow.

E. Seasonal Influence. The data obtained on feeding movements could be used to examine the effect of seasonal weather. The average movement was nearly the same for three seasons (7.0, 7.1, 7.45) with the winter average (4.59) being considerably less. Using the X^2 test for independence between the four seasons and distance groups of 2 ft. and less, and 3 ft. and more, a value of 13.1 ($P < 0.01$) was calculated. Deviations from expected values in the winter and fall seasons contribute most to the chi square value.

F. Temperature and Vapor Pressure Deficit. A more elaborate chi square test was designed, but is not included here, that not only checked association of temperature and vapor pressure deficit with distance of movements, but also examined the type of variation with temperature while pressure deficits were held constant and checked deficit effects while temperatures were held constant. The data were first divided into four temperature categories, and then within each of these groups a test was made for an association between distance of movement and vapor pressure deficit. In temperature ranges 65-70 and 71-76° F a significant association was shown between greater distances and lower deficits; this was not shown for temperature ranges 54-64 and 77-82° F. When data from all temperatures were totaled, a real connection was illustrated between greater distances and lower deficits, i.e., the toads tended to move further with lower pressure deficits. A test for heterogeneity of frequency distributions of movement plotted against pressure deficits indicated that the direction of frequency variation was homogenous under the four temperature groups.

In a similar analysis the data were first separated into four pressure deficit categories and then, under each of these, associations were tested between movement and temperature. Distance of movement and temperature were associated under pressure deficits between 0.02 and 0.059 in. and greater than 0.12 in. Hg. but associations were not significant in deficit categories 0.00-0.019 and 0.06-0.119 in. When deficit categories were lumped a significant association was shown between temperatures and distance of movement. A test for heterogeneity of frequency distributions under the four deficit categories indicated that the frequency distribution of distances against temperature is homogeneous under the four pressure categories.

SPATIAL RELATIONSHIPS

SPATIAL DISTRIBUTION

A more detailed examination of the spatial distribution of toads was undertaken in plot 1 when it was observed that the concentration of toads was uneven

in the pot. General observations indicated that there was a tendency towards aggregation in the ecotonal areas, especially where the low shrub and herbaceous vegetation was sparse. There were almost no captures of toads in areas where the shrubs were dense, as, for example, between lines L and K extending through the western two-thirds of the plot (Fig. 1). In the more open areas of the hammock, as between lines L and O, the density seemed to be between that of the ecotone and the area of dense vegetation. Following procedures outlined by Dice (1952), a test of spatial distribution in plot 1 was made for data collected between July 26 and December 30, 1951. This selection of material was made because after December, 1951, observation was not concentrated uniformly over the plot. The area was divided into quadrats 25 ft. square and for each night's data the number of quadrats in which 0, 1, 2, 3, n individuals were caught was recorded. The results of the study are given in Table 8. A chi square test yielding a value of 399 gave strong evidence ($P < 0.01$) that the distribution did not follow a Poisson type. Dice (*ibid.*) stated that if the distribution was not random and the variance was greater than the mean, an aggregational phenomenon was denoted. Here the variance was 4.68 and the mean 2.05; thus aggregation within this plot was statistically shown.

TABLE 8. An analysis of spatial distribution of toads in plot 1. The frequencies are the number of quadrats per field trip totaled for the study period.

Number Individuals per Quadrat	25' Units	10 SQUARE FOOT QUADRATS			
		Total Burrows	Burrows, Sum, '53	Captures, Ecotone	Captures, Hammock
0	78	1,517	51	6,006	2,864
1	53	173	30	998	262
2	37	15	7	104	8
3	30	...	2	18	...
4	19
5	11
6	11
7	6
8+	8
Total	253	1,707	90	7,126	3,134
Mean	2.11	0.119	0.556	0.1768	0.0859
Variance	4.68	0.135	0.536	0.1899	0.0887

A test for aggregation within a homogeneous habitat was made utilizing the techniques above, except that quadrats 10 sq. ft. were used in the surveyed ecotonal and hammock areas. The locations of known burrows in the ecotone were plotted for each month of study, and when the monthly totals were added, they formed a distribution not different from a Poisson type ($X^2 = 1.74$). The burrows of the active population were studied most intensively and were best known during the summer 1953 and when these were plotted, the distribution was not significantly different from a random one ($X^2 = 0.20$). However, there was a slight indication that these burrow loca-

tions were more evenly spaced than in a random distribution.

The capture sites in the hammock were located on the 10 ft. grid system for night trips and a test for deviation of the distribution gave evidence that it was of the Poisson type ($X^2 = 1.4$). Therefore the surface activities of toads in the hammock were such that individuals were randomly distributed in space.

However, a similar test of the spatial distribution of capture sites in the ecotone, when data were treated as above, indicated a statistically significant deviation from the Poisson type distribution ($X^2 = 33.03$). Factors involved in this aggregation in surface movements are unknown, but there appear to be more captures just inside the ecotone and near a fallen mass of twigs, leaves, and other debris near i-9 in Fig. 1. Possibly the tendency towards aggregation in the ecotone resulted from movements to optimal feeding locations, and the habitat was not homogeneous with respect to food supply. If a shortage of food existed in the higher density of this ecotone, the toads might be forced to gather in the more favorable feeding locations.

HOME RANGE

A home range can be defined as "the area over which an individual animal habitually travels while engaged in his usual daily activities." This definition by Dice (*ibid.*) is applicable to the following discussion, except that in the present work movements associated with breeding were excluded from consideration of home range. He gives a good general discussion of the home range concept and methods of its study; he also says that, "Relatively little is known about the home ranges or territories of amphibians and reptiles."

The method of determination of home range size in the present study was the "minimum-home-range" method that produces more consistent and reliable results than other variations of the technique, according to Mohr (1947). It involves plotting the capture locations and connecting the outside points to form an irregular polygon. The area of this was calculated, providing an estimate of range size. This method was especially applicable since captures of individuals were not restricted to traps in a grid system, but were spatially at random; thus a more accurate picture of the utilization of space was given. A standard for conversion of paper weight to area in square feet was established by weighing 25 pieces of paper cut to scale to 0.0001 gm. Care was taken to use paper with a low coefficient of variation. Paper representing the home range was weighed and the conversion to area made.

The average home range of 88 individuals in plot 1 that had been captured more than six times was 108.4 sq. ft. with a range from 7.1 to 892. The average for males, 91.2, was smaller than for females, 111.5, but the difference between means was not statistically significant.

One or more capture sites of most individuals were

considerably apart from the others, which tended to be clustered. Apparently if the home range represents the average utilized range, a more accurate picture of the amount of space used would be obtained, if the 10% of total captures that represented extreme wanderings were eliminated. Using only the remaining 90% of capture locations, the mean range area was 67.7 ± 6.9 , the variation being from 2.6 to 356 sq. ft. The average home area of 39 males was 60.8 ± 9.9 while that for 49 females was 73.5 ± 9.3 , that for the males being smaller; but again the difference lacked statistical significance.

The distance of movement for food was greater in the ecotone than in the hammock; therefore it was not surprising that the average of 68 ecotone home ranges, 119.7 ± 17.5 , appeared to be greater than that for 20 hammock ranges, 83.3 ± 13.7 . The difference lacked significance. It has already been shown that movement distances in feeding operations, and by inference also home ranges, were less under higher densities in the semi-controlled populations. It will be shown later that the density of the ecotone was about double that of the hammock, and therefore it follows that the ecotone home ranges should be less rather than greater than the hammock, as they actually were. On the other hand, it seems that toads in an uncontrolled situation would be found in greater densities in the more optimal habitats. The ecotone would thus be a more suitable general habitat, and movements should be greater under optimal rather than sub-optimal conditions.

Several statistical analyses of the connection between the length of time that individuals were under observation and their home range size, indicated no statistically significant correlations or associations. Examination was made of the relationship between size of range and the number of captures for toads, and a significant ($P = 0.01$) correlation coefficient of 0.34 was determined for the relationship. Then, the data were placed in categories of 7 to 12, 13 to 18, and 19 and more captures; while the ranges were grouped into less than 50, 50 to 100, and greater than 100 sq. ft. and a significant association was revealed between size of area and number of captures ($X^2 = 23.7$, $P = 0.01$). The number of captures, and indirectly the time factor, must be considered in statements of home range size.

Many toads moved their burrows one or more times within their home range. The average area of the 37 toads for which only one burrow was known was 65.0 ± 11.3 . This was significantly less than that for 39 with more than one recorded hole, 123.8 ± 16.8 . In the analysis of home range the observer then should consider data on the shift of burrow locations.

Records are available on 89 shifts of burrow location made by 39 spadefoots. The average distance the site was moved was 10.8 ± 0.77 ft. with a recorded range from 2 to 38 ft. The times of movement were not associated with any particular climatic or seasonal phenomena. The average time that burrows of these 39 toads were used was 115 days. This had little

biological significance, however, since 29 of them were used only one night, while ten were occupied more than one year, and one was recorded in use for 713 days. No evidence was obtained that more than one toad uses the same burrow.

Thirty-one individuals moved their burrows to one or more new locations within the home range, but did not return to the original ones. Eight of the toads alternated their utilization of from 2 to 5 burrows. For one period they would emerge from burrow A, then for a second interval use burrow B, then C, and finally return to use A or B. Illustrations of this are as follows: Fig. 5, #104₅—2 burrows, #1155—4 burrows; Fig. 6, #1305—two, and #3241—2 burrows. As further illustration data on #104₅, #1155, and #120 are given in Table 9. Careful study of these records, especially for the 1953 summer period, when almost daily visits were made, will show that these toads did not use any one burrow for any extended time. The records of #120 and #1155 indicate that there was fairly equal use made of the several holes involved.

TABLE 9. Records of burrows shifting and alternation for three individuals from plot 1.

Animal Number	Burrow Number	Location	Dates Used	Captures	Days
104 ₅ ♀	I	5 NNW G-3	3-13-52 to 6-29-53	17	473
	II	4 SSE F-2	7-2-53	1	1
	I	5 NNW G-3	7-10-53	1	1
	II	4 SSE F-2	7-16-53	1	1
	I	5 NNW G-3	7-21-53 to 8-11-53	6	21
	II	4 SSE F-2	8-17 to 8-18-53	2	2
	I	5 NNW G-3	8-19 to 8-27-53	4	8
120 ♀	I	12 SSE O-2	12-30-51 to 6-3-52	4 (+37)	155
	II	2 S O-2	8-28 to 9-2-52	2	5
	I	12 SSE O-2	9-12 to 10-8-52	2 (+27)	26
	II	2 S O-2	4-26 to 6-24-53	8	59
	III	3 NW O-3	7-6 to 7-7-53	2	2
	IV	5 E M-2	7-10 to 7-14-53	2	4
	V	4 N M-2	7-18 to 7-21-53	2	3
	IV	5 E M-2	7-25 to 7-26-53	2	2
	II	2 S M-2	8-10 to 8-12-53	3	3
	V	4 N M-2	8-16 to 8-18-53	3	3
	IV	5 E M-2	8-21 to 8-22-53	2	2
1155 ♀	I	1½ WSW E-2	10-14-52 to 6-6-53	7	235
	II	4 SSW E-2	6-24-53	1	1
	III	5 WSW E-1	7-8 to 7-14-53	2	6
	II	4 SSW E-2	7-16-53	1	1
	III	5 WSW E-1	7-23-53	1	1
	IV	3 WNW E-3	7-26 to 7-27-53	2	2
	III	5 WSW E-1	7-31-53	1	1
	IV	3 WNW E-3	8-10-53	1	1
	III	5 WSW E-1	8-16 to 8-18-53	2	2

Examination of home range shapes formed by connecting the outside points of captures allowed the following breakdown: circular or square, i.e., #443 in Fig. 6, 11 ranges; rectangular or rectilinear, i.e., #1305 in Fig. 6, 39 ranges; essentially linear, i.e., #1004 in Fig. 6, 34 individuals, and triangular, 4 ranges. A summary of burrow locations within the 88 ranges studied in plot 1 showed that 20 had a central location, while 109 were located peripherally.

Examination for overlapping of ranges for toads of the same sex in the most crowded portion of the

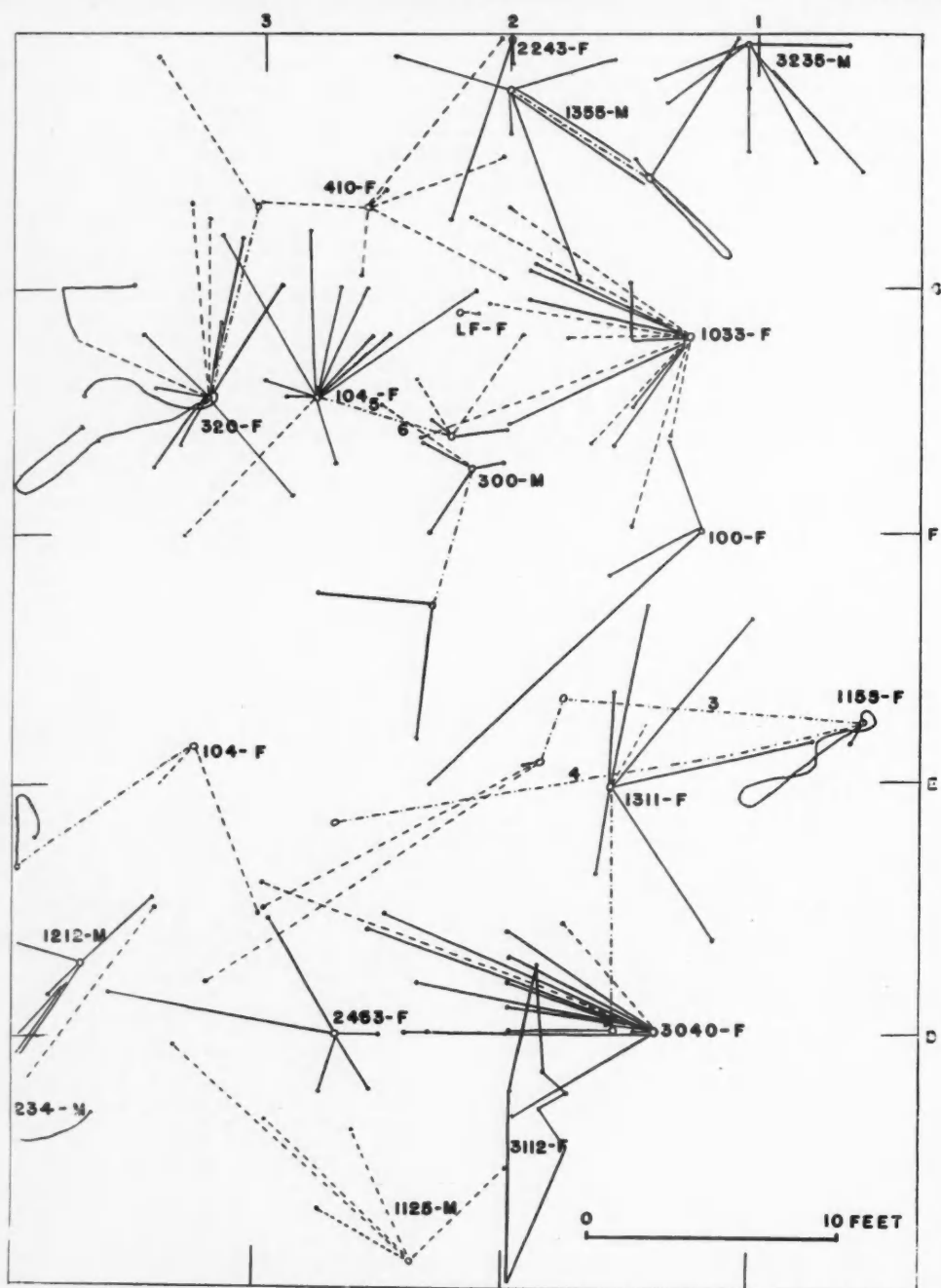


FIG. 5. The home ranges of individuals in the most crowded part of the hammock in plot 1. o = burrow; — connects capture sites with known burrow; --- burrow use assumed; ··· movement of burrow site; number over latter indicates times burrow use alternated. North is toward the bottom, west to the right.

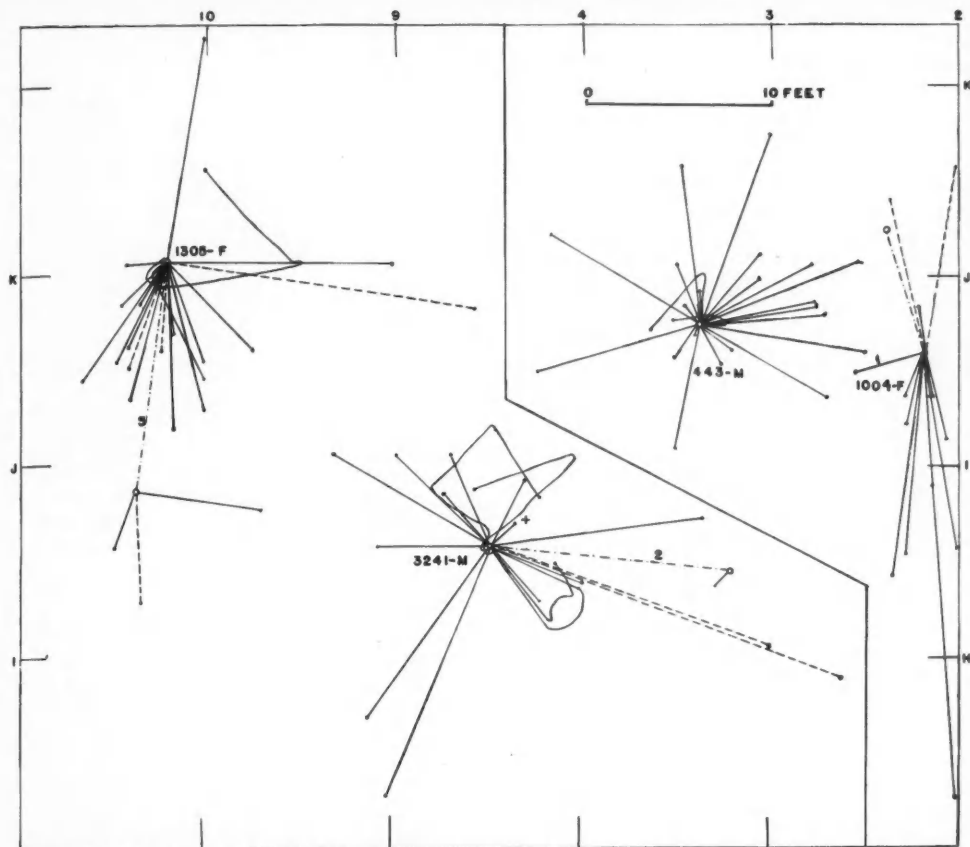


FIG. 6. Home ranges of selected individuals from the ecotone in plot 1. The symbols are similar to those in Figure 5.

hammock, indicated that there was no overlap. A similar study for areas of highest density, i.e. the ecotone in Fig. 5, shows that there is only a slight overlap between several of the individuals. The overlap that does exist is only apparent as the ranges did not overlap in the same time period.

From the ranges shown in Fig. 5 possible avoidance reactions were noted. Observe that in movement of its burrow, #1155 crossed the range of #1311 on two separate occasions. A female, #120 in the hammock twice moved its burrow southward (Table 9), and apparently avoided the ranges of a male and a female resident.

The existence of a homing reaction in which individuals returned long distances from breeding grounds to exact locations of departure was demonstrated by the capture of 7 individuals before, during and after the breeding on April 7, 1953 (Table 10). The toads were caught and positively identified (1) in the plot, (2) either in the breeding areas or between them and the plot, and (3) again in the home area; this definitely indicated a homing movement.

A more circumstantial type of evidence gathered

during the reproductive period concerning homing behavior was obtained by observation of females. The records showed that #1045, #1155, and #1030 (Table 10) had observable ovarian eggs when they were caught before breeding, and they were later captured at or near the same home location with no eggs. The assumption was made that they traveled at least several hundred feet to the nearest pool, deposited their eggs, and then returned to their home area.

A few records were obtained (#2245, #100, #3244 in Table 10) during the breeding period of August 24, 1953, from the trap system located east of plot 1. The animals were trapped as they were leaving the plot, and after their release, they were subsequently caught in another trap, denoting that their movement was towards the plot.

Light can be shed on the relationship between movement within the home range and the type of micro-habitat. In Fig. 5 between lines 1-4 and from line D to south of line G, the habitat was homogeneous with almost no herbaceous or shrub vegetation. West of line 1 and north of line D the ecotone was composed of a dense growth of herbs and shrubs.

Table 10. Data on captures indicating a homing reaction.

Number	Date	Capture Location	Observations
4	3-21-53	1 SW I-9	Calling in pond, 700' from above 25' from departure point
	4- 7-53	300 SW C-1	
	4-12-53	3 NE K-7	
300	3-11-53	4 NE F-2	At burrow
	4- 7-53	¼ mile SW plot	Calling in breeding chorus
	4-12-53	4 NE F-2	At burrow
1104	3-11-53	5 S O-1	350' from home area In burrow
	4- 7-53	200 SW C-1	
	6- 9-53	12 W O-1	
1125	11-13-51	10 NNW D-2	In burrow
	4- 7-53	300 SW C-1	Swimming in pond
	6-29-53	2 S H-9	Near probable departure point
	7- 2-53	6 NW D-3	
1304	3-31-53	8 SSW B-4	In burrow
	4- 7-53	150 SW C-1	About 600' movement
	5- 5-53	7 SSW B-4	
2215	6-27-53	30 W C-4	About 900' from probable departure Female spent, eggs gone
	4- 8-53	500 NW B-1	
	6- 8-53	45 W C-1	
2313	3-21-53	1 E H-7	
	4- 7-53	200 SW C-1	
	7-26-53	10 NNE H-7	
1045	3-11-53	1 E G-2	Eggs in body cavity
	4-26-53	5 NNW G-2	Few eggs
1155	3-11-53	1 SW E-2	Many eggs in body cavity
	4-26-53	2 SW E-2	No eggs
1030	9- 2-51	C-1	Eggs in body cavity
	4-12-53	15 W C-1	No eggs
2245	8-14-53	7 SW O-5	Released east of trap system Apparently moving westward
	8-25-53	Trap W	
	8-26-53	Trap E-1	
100	8-21-53	2 E F-1	In burrow
	8-24-53	3 SE E-3	Moving away from plot?
	8-25-53	Trap W	Trap adjacent home range area
	8-26-53	Trap E	Returning direction to home site
3224	4- 9-53	15 S K-3	Returning towards plot? Movement into plot continued
	8-25-53	Trap E	
	8-27-53	2 NW E-2	

The movements from burrows of #1033, #3040, and #1125 were all in the direction of the open areas and away from the dense vegetation. The radiation from burrows of #320 and #104₃ was much more nearly symmetrical and was located entirely in one phase of the habitat. There was a lower toad occupancy in the portions of densely vegetated ecotone than in open habitat.

In Fig. 6 the movements of #1305 were nearly all clustered in one area north of the burrow. This area coincides with a mass of dead leaves, twigs and rotten wood. The correlating factor between sites of capture and debris probably was food. The movements from the burrow by #1004 were mostly towards the ecotonal break between hammock and prairie, and they produced a linear shaped range.

The curve lines connecting capture points with

burrows of some individuals in Figs. 5 and 6 were the paths followed by toads on their return to the burrow after capture. It was normal for toads to move in a direction away from the burrow, to turn sharply one or more times, and then to proceed to the burrow. The approach was seldom direct. It was usual for the animal to circle the burrow from 270 to 360 degrees before entering, when about 2 to 4 in. from the aperture.

Observation of many approaches by toads to their burrows showed that they were spatially well orientated when near them, and there was little or no apparent hesitation in moving into the hole. On several occasions individuals backed from several inches distance into an aperture that was hidden beneath a large, fallen leaf or a mat of leaves.

DISPERSAL

One method of analysis for the rates of movement or dispersal of the adult population was the study of the percentage of new animals taken each field trip. Theoretically after a preliminary period all of the animals in the population would be marked, and the retake percentage, or the proportion of the catch that had been previously marked, should approach 100. Actually some new toads were taken even at the end of the study, thus representing continued immigration into the area. Since for consecutive census periods the population density remained approximately the same, it follows that nearly the same number of animals had emigrated.

Retake percentage plotted against the cumulative number of hours in the field is given in Fig. 7. The curve rose rather rapidly beginning in July and extending through August, 1951, before it dropped suddenly during the heavy rains and breeding of September, 1951. It rose again in October and remained nearly constant until February, 1952, when it dropped considerably during a period of heavy rains and another slight breeding season. The curve reached a peak of 100% in April and a low of 50% in May, 1952. The higher retakes between 80 and 90 hours represented study done in the hot dry summer of 1952. Lower percentages came during the wet fall of 1953, with slightly higher values for the winter period. Heavy rains and an extensive breeding in early April were correlated with the drop to below 50% retakes after about 120 hours' work. Following this shift in the population, the retake percentage climbed and remained high during the intensive field work of the summer of 1953, until it fell during breeding in August. Four of the five major declines in retake per cent occurred during breeding seasons and times of extensive rainfall.

New toads were recorded much less frequently during the hot dry summer of 1952 and the cold dry winter periods than during the wetter spring and fall seasons. In the summer of 1953, the amount of rainfall was measured and toads were observed on 44 nights from June through August. A χ^2 test using categories of rainless as compared with days of some

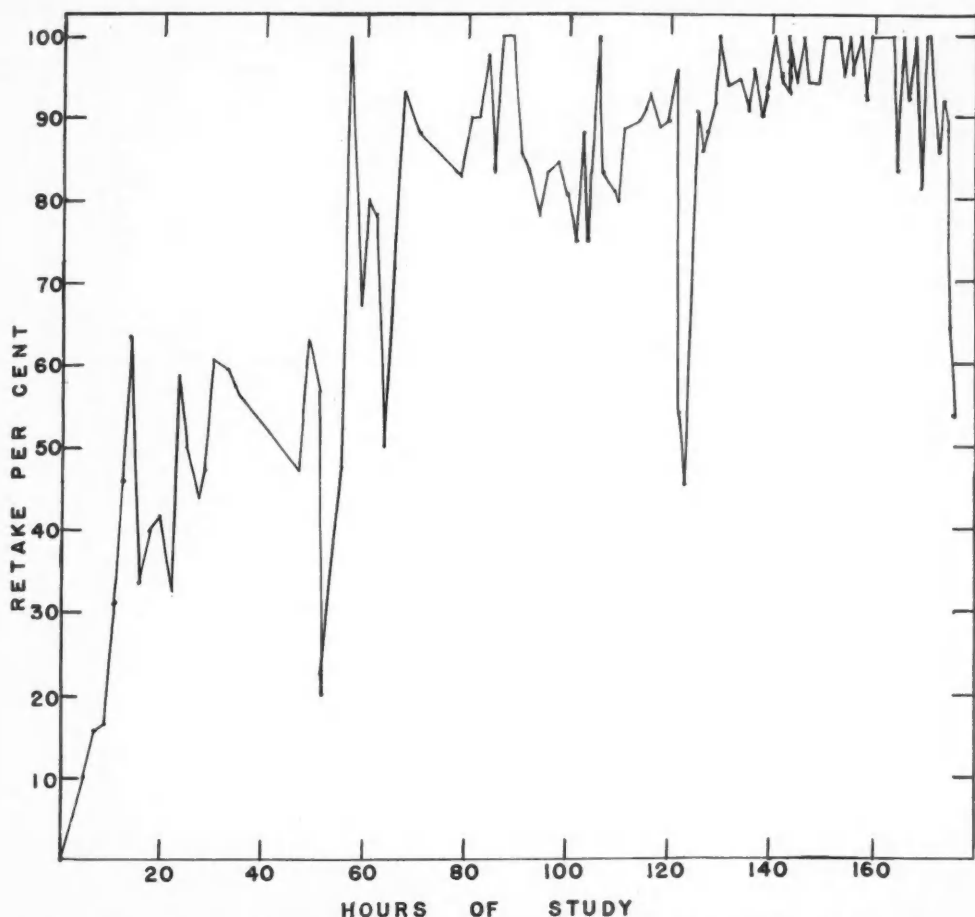


Fig. 7. Changes in percentage retakes in plot 1 in relation to the cumulative number of study hours.

rainfall and days of 100% retakes contrasted with less than 100% retakes denoted an association between the immigration of new toads and days of some recorded rainfall ($X^2 = 4.7$, $P < 0.05$).

During this summer period between June and August, 1953, the trap system was in operation at the east end of plot 1 to test amounts of dispersal. Twenty captures were made in this trap between June 1 and August 22, only one of which represented an animal previously marked in the plot. These 20 captures occurred in connection with wet, rainy days. From August 23 through 27 results indicated that the major dispersal occurred during breeding periods.

Heavy rains connected with a stationary weather front fell on August 21-23, 1953, and in mid-afternoon of the latter day breeding choruses of the spadefoots began. Successful breeding in the ponds 300 ft. SW C-1 and $\frac{1}{2}$ mile southwest of the plot was denoted by neural-groove stage tadpoles the following afternoon. Traps were checked for dispersal movements at 2 p.m. August 24 and 6 toads were caught in the south, 3 in the east, and one in the north quad-

rants of the system. Since it was assumed that if toads were trapped in the south quadrant of the system, they were heading in a northerly direction, the results reflected a major movement from the south towards ponds in the prairie. Toads trapped in a quadrant were released in the opposite one, midway between the open arms of the trap fences.

Heavy rains continued the night of August 24, but only non-breeding males were seen in the ponds southwest of the plot. Many toads were heading through the plot from the direction of the prairie towards the southwest. Many were slimy and they seemed to be moving away from the breeding areas. The migrations were checked this night by trap inspection the next morning and 14, 72, 50, and 25 animals were caught respectively in the north, east, south and west quadrants. The relationships of the trap with the prairie were such that captures in the north and east quarters seemed to represent movements from the prairie whereas for the other half of the system the opposite was true. It appeared that a great deal of traveling in all directions occurred this night, and the

majority of toads were heading away from breeding areas in the prairie.

The trap results for the nights of August 25 and 26 were such that no conclusions could be made concerning the major direction of movement. However, 11 captures gave data on directional movements of toads trapped in opposite quadrants on August 23 and 24 for there was a greater percentage of released toads returning in a southerly and westerly direction than otherwise. These were probably trapped the first two days as they moved towards the prairie to breed, and then on the latter two days after the breeding was finished they were moving back to the south and west toward their home areas.

Ten of the toads trapped on August 24 had been marked in the plot earlier. Taken in the east quadrant (on the side opposite the plot), were: #1043, last taken October 8, 1952, at 3 SW N-5; #1440, last observed December 3, 1951, at 20 S K-11; and #3223, captured April 9, 1953, at 15 S K-3. A toad last seen April 9, 1953, was trapped in the south quadrant. These toads taken on the other side of the trap from the plot had not been observed as residents in the plot for considerable periods of time. Six toads, marked in the plot and seen there during the summer, were taken in the western quadrant that was nearest the plot. The location of last capture for each of these six and the corresponding date of observation were: 3 E J-10, 6-30-53; 7 SW O-5, 8-14-53; 10 SSW G-1, 8-19-53; 2 S D-5, 8-24-53; 3 SE E-3, 8-24-53; and 3 E H-9, 8-22-53. Two of these were seen in or near their home range the same night that they were later trapped when moving out of the plot.

In Table 11 data from plot 1 on dispersal as measured by the greatest distance between captures for particular time units are listed. Greatest distances for monthly units were totaled in the four groups given in the table. When the greatest known dispersal distances for the study were plotted, it was seen that the bulk of toads did not move more than 32 ft. A breakdown of time intervals for movements that were not known to be directly correlated with breeding was made. One 200-ft. movement took place in nine days or less; 123, 125, and 250 ft. movements took place in approximately one month's time, and all of the others had long periods between captures.

Data in Table 11 lead to the conclusion that most of the dispersals were of relatively short distance, and they accounted for the gradual addition of new toads in the study area. Shifting of the population components occurred in greater amounts during the fall and spring seasons, and was probably most directly correlated with rainfall. The greatest measured amount of population shift occurred a day or so before, during, and shortly after breeding activities.

POPULATION DENSITY

TECHNIQUES OF ANALYSIS

One major problem in this part of the investigation was estimating population density under field conditions. An excellent opportunity to study various

TABLE 11. Results of an analysis of maximum distances between capture-sites in plot 1.

Distance Feet	Entire Study	SEASONS				MONTHS			
		Winter	Spring	Summer	Fall	Dec.-Feb.	Mar.-May	June-Aug.	Sept.-Nov.
1.....	30	20	17	28	14	7	9	45	9
4.....	33	17	20	18	19	8	13	27	8
7.....	25	14	19	26	11	9	10	24	6
10.....	39	7	15	28	16	2	9	44	10
13.....	32	4	10	14	6	2	7	19	—
16.....	38	—	12	20	7	1	5	23	2
19.....	32	3	5	14	7	1	2	13	2
22.....	24	2	1	8	2	1	—	8	1
25.....	17	—	2	5	5	—	3	3	—
28.....	11	—	1	5	1	—	—	3	1
31.....	16	1	1	5	1	—	1	3	—
34.....	9	—	1	—	1	—	—	—	2
37.....	1	—	1	2	2	—	—	2	1
40.....	3	—	—	1	1	—	—	—	—
43.....	3	—	—	—	—	—	—	—	—
46.....	5								
49.....	3								
52.....	2								
55.....	6								
58.....	2								
61.....	6								
64.....	4								
67.....	2								
70.....	3								
73.....	1								
76.....	—	4	5	8	9	—	—	4	1
79.....	2								
82.....	1								
85.....	1								
88.....	—								
91.....	2								
94.....	1								
97.....	2								
100.....	2								
103.....	5								
106.....	1								
107+.....	31								

estimation techniques was available in plot 3 where there was a known beginning-population density.

The most obvious method of density determination is to count the number of individuals per unit area. Since toads spend a great deal of time underground, it is impossible to make this simple count. In pen 1 of plot 3, 40 individuals were introduced. Cumulative data on the number of these that were observed and known to be present after a given number of observation periods were, respectively, 19, 3; 21, 5; 23, 8; 27, 14; and 29, 17. That meant that even after the pen had been searched 17 times only 72.5% of the population had been captured. After this length of time emigration and immigration would have changed the original population if it had not been enclosed by fence, and mortality would in any case have changed its size.

One modification of this method was to add to the number actually counted those toads that were taken in periods both before and after the one under con-

sideration. The animals could not leave the fenced areas of plot 3, so that if a toad was taken late in the study it must have been present continuously from the beginning. In plot 3 this estimate for a particular period improved as later work reported the presence of individuals, and the adjusted count was probably lower than the actual population size for the latter part of the study. Using this method in the natural populations required the assumption that if a toad was taken before and after, but not during a particular period, it had been present in the area but had remained unobserved during the interval.

Using capture records of marked and released individuals several statistical methods are available to estimate the population. The method sometimes known as the Lincoln Index, discussed by Dice (*op. cit.*), utilized results of two successive field trip records. The formula may be written:

$$P = \frac{X}{Y}$$

where P is the population size at the time of the first trip, X is the number of toads marked the first night, and Y is the proportion of the second night's catch that was marked on the first trip.

A revision of this method was used by Hayne (1949 b), that provided a way of averaging all estimates for sets of paired field trips. This suggestion was based on the idea that the percentage of retakes for any particular observation varies directly with the number of animals previously marked in the population. The formula is:

$$Y = \frac{X}{P}$$

where P is the population size, X is the number of animals previously marked and released, and Y is the proportion of the population marked. To obtain an estimate, one must find the trend line that best fits this relationship for the results of the census period. The trend line shown in Fig. 8 that passes through the origin on the X and Y axes, can be drawn by eye or obtained by statistical means. Hayne (*ibid.*) gave the following formula to obtain an estimate of population size directly:

$$P = \frac{\sum WX^2}{\sum WXY}$$

where the repeated variables are as defined above and where W is the number of captures per field trip and where \sum calls for summation of data from each of the field trips.

Assumptions inherent in this method were discussed by Hayne (*ibid.*), Dice (*op. cit.*) and others. To use these methods one must assume that there is an equal probability of capture of marked and unmarked animals. In order that an equal probability of capture is found there must not have been any significant additions to the population during the census period either by reproduction or by immigration. Also, marking must not cause differential mortality or emigration. Finally behavior relative to capture or observation must be such that marked animals are not caught with greater ease than unmarked, or vice versa.

A more recent method, using a mark-and-release index B , has been used in which the assumption of an equal probability of capture for marked and unmarked animals need not be made (Tanaka, 1951, 1952, Tanaka & Teramura, 1953). Tanaka (1952) proposed a justification for this method and showed how the index B can be obtained from field data. The basic equation used by Tanaka is:

$$Y = \left(\frac{X}{P}\right)B$$

where X , Y , and P are defined above and B is the mark-and-release index. If $B = 1$, the equation is rectilinear; the probability of recapture is equal for marked and unmarked animals, and it is the equation used by Hayne. If B is greater than 1, the probability of capture is greater for unmarked than for marked individuals. If B is less than 1, there is greater probability of capture for marked than for unmarked toads, and the resulting curve and its relationship to the trend line when B is 1, is seen in Fig. 8. It is noted that when B is different from 1, the equation becomes curvilinear. Factors that regulate the probability of capture for marked and new animals will influence this index. In the present study, the test was whether marked or unmarked individuals were more liable to observation and capture. This could be affected by a tendency for the observer to see animals of known home range or burrow location more than unfamiliar ones. It could also be influenced by immigration and emigration of animals.

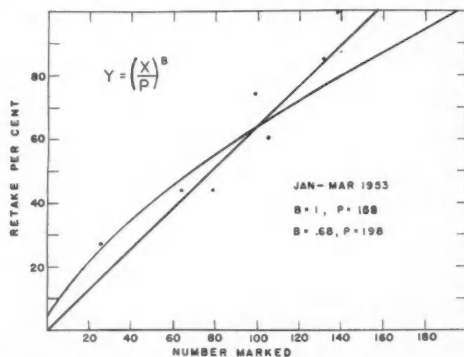


FIG. 8. The relationship between rectilinear and curvilinear methods of population density estimation when B is less than 1.

The data from plots 1 and 3 were placed in census periods and analyzed with the above methods. It was desirable not only to have a sufficient number of field observations in a census period so that the data could be better studied statistically, but also to have periods that group results as nearly homogeneous to seasonal, climatic, and biological factors as possible. Within a census period a toad was considered as "unmarked" or "new" if it had not been observed, and "marked" if it had been taken earlier during the particular census period.

CENSUS RESULTS

Data from plot 3 are given in Table 12 with the exception of results of work done after August, 1953, and of dates on which no toads were observed. These data were used to obtain the estimates of population size given in Table 14. It appears that the adjusted count was the most reliable measure for plot 3 populations and that the greatest error in this count was during the last census period. The simple count of the number of toads was considerably below that of the adjusted count in three of the five census periods, and was especially low during the two summer periods. These two counts of the population were nearly the same for the periods from January through June, 1953, when the amount of activity was high.

The statistical method proposed by Hayne (1949 b) produced results that tended to underestimate the population size. This was especially noted during the two summer periods where this index estimate of population size was lower than the adjusted count by 25 and 20 (Table 14). The method of population measurement given by Tanaka (1952) produced estimates that were not greatly different from the former ones except during the last period of the summer of 1953. During that summer, the mark-and-release index was much less than one, indicating that the probability of capturing previously marked animals was greater than for new ones.

Associated with the low estimates of the population attained by the index methods during the summers of 1952 and 1953 was an especially low amount of toad activity. If the probability of capture is the same for all individuals in a population during a particular census period, the population estimates should not vary with the amount of total toad activity. It was known that rates of toad emergence varied from season to season and from one type of weather to another. It was assumed that the probability of emergence for any individual toad in a census period would be proportional to the number of emergences for the total population. If this were true, the marked toads would mix at random in the captured population and amount of activity would not seriously influence the index estimates.

The assumption was not valid. General observations during these summer periods indicated that toad captures were of a small segment of the total population, and the remainder of the total did not appear in the sample at all. Similar information was obtained by study of emergence and non-emergence from burrows in plot 2 from June through August, 1952. The burrows of ten toads were observed and from these only five animals were active during the summer period. Of these five, one emerged ten times in a period of 33 nights; another came out four out of eight nights; a third emerged four in a span of 25 nights; another was recorded twice in ten nights; while the last was active only one night during the summer. The activity of these toads was condensed into relatively short periods.

A further test was employed for data from plot 3

TABLE 12. A summary of field census data from plot 3.

Period	Date	NUMBER OF CAPTURES			Proportion Previously Handled (Y)	Number Previously Handled (X)
		New	Previously Marked	Total (W)		
1	July 23, 1952	30	..	30		
	July 24	10	13	23	.57	30
	July 25	4	12	16	.75	40
	Aug. 11	4	17	21	.81	44
	Aug. 12	2	11	13	.85	48
	Aug. 29	—	2	2	1.00	50
	Aug. 31	1	8	9	.89	50
2	Sept. 8, 1952	9	..	9		
	Sept. 17	9	2	11	.18	9
	Sept. 22	3	1	4	.25	18
	Sept. 23	10	4	14	.29	21
	Oct. 7	8	6	14	.43	31
	Oct. 17	9	12	21	.57	39
	Oct. 18	3	10	13	.77	48
	Nov. 10	3	13	16	.81	51
	Dec. 10	—	3	3	1.00	54
	Dec. 20	3	18	21	.86	54
3	Jan. 8, 1953	4	..	4		
	Jan. 20	18	1	19	.05	4
	Feb. 3	17	12	29	.41	22
	Feb. 11	2	5	7	.71	39
	Feb. 25	7	14	21	.67	41
	Mar. 3	4	12	16	.75	48
	Mar. 10	—	6	6	1.00	52
	Mar. 12	8	32	40	.80	52
	Mar. 18	7	18	25	.72	60
	Mar. 23	2	39	41	.95	67
4	Apr. 1, 1953	10	..	10		
	Apr. 10	25	6	31	.19	10
	Apr. 24	6	8	14	.57	35
	May 1	9	15	24	.625	41
	May 6	2	7	9	.78	50
	June 3	8	13	21	.62	52
	June 10	3	16	19	.84	60
	June 15	1	19	20	.95	63
5	July 1, 1953	3	..	3		
	July 9	1	—	1	.00	3
	July 15	2	1	3	.33	4
	July 18	3	1	4	.25	6
	July 20	3	8	11	.73	9
	July 29	—	2	2	1.00	12
	Aug. 6	4	7	11	.64	12
	Aug. 11	—	1	1	1.00	16
	Aug. 20	3	7	10	.70	16
	Aug. 23	7	13	20	.65	19
	Aug. 26	1	5	6	.83	26

using records of 26 animals caught in pen 1 and known to be present from July, 1952, through June, 1953. In this test it was assumed that each individual would be captured in proportion to the number of field trips in each period of : (1) July-August, (2) September-December, 1952, (3) January-March, and (4) April-June, 1953. For example, if an individual was captured a total of ten times during the year, and if 20% of the total field work was done in the first period, it was expected that the toad should have been caught twice during that first period. A chi square value was calculated, then, for this individual for this first period using the formula:

$$X^2 = \frac{(\text{Observed} - \text{Expected})^2}{\text{Expected}}$$

were not observed at random with regard to the four periods studied. The number of toads not observed in each period and the weighted average number of times the active toads appeared were, respectively: July-August, 14, 3.10; September-December, 13, 2.08; January-March, 2, 2.96; April-June, 5, 2.32. In the summer, over half of the cohort was not observed, but those toads that were active were seen a greater number of times, on the average, than for any other season.

Thus it appears that during some seasons, i.e. summer 1953, only a small part of the total population is active and these individuals tend to emerge a greater number of times in short periods than at other times. The index methods under these conditions would underestimate the true population size.

The B index figures shown in Table 14 are for the most part very near one. Only one index, that for April to June, 1953 in plot 1, greatly exceeded one. This period followed the breeding of April 7, and the high chance of capture for new animals reflected the immigration associated with breeding migrations.

Of the indices lower than one in both plots, the majority occurred during the summer, especially the summer of 1953. These resulted from (1) less immigration and emigration of the population, (2) smaller numbers of active toads that tended to emerge more times, thus increasing the captures of animals previously handled, and (3) the smaller active population increased the chance for the toad locations and habits to be learned by the observer.

An adjusted estimate of the plot 1 population was calculated, using a simple proportion between the Tanaka estimate for plots 1 and 3, and the adjusted count for plot 3. The assumption required was that toads in plot 3 would react to environmental factors essentially in the same manner as those in the wholly natural situation. Since the proportion and direction of error in the Tanaka estimate for plot 3 were known, the theoretical population of the natural site could be estimated. The major source of error comes from the incidence of immigration-emigration that affected the recapture index in plot 1. This error can be detected in Table 14 for the April-June, 1953 period, where high population dispersal caused a very high B value (1.64) in plot 1, while the same figure for plot 3 was less than one.

A breakdown of population estimates for the hammock and ecotone habitats in plot 1 is given in Table 15. These data, like those in Table 14, were probably underestimated for the summer census periods, using the Hayne index method, and were low for the first and last periods, using the adjusted count technique. Examination of the conversion to toads per acre indicated that the density of the ecotone was about double that of the hammock except during July and August of 1953. During July, 1953, the apparent density in the hammock exceeded that in the ecotone; the explanation for this exception is probably that it results from poor sampling. The greatest error in the adjusted count method came during the last periods of

the study. The apparently higher density in the hammock may result from lower activity rates for ecotonal toads, which in turn would decrease the number of toads known to be present in the ecotone during this latter period. The density of plot 3 was about twice that of the total census area of plot 1. It should be mentioned that the three density levels of plot 3 in toads per acre were 2,192, 1,096, and 548 at the beginning of the experiment. Therefore, the lowest beginning density level in plot 3 was a little higher than the highest estimates for plot 1.

TABLE 15. Population estimates for two habitats in plot 1.

Census Periods	HAMMOCK			ECOTONE		
	Hayne Estimate	ADJUSTED COUNT		Hayne Estimate	ADJUSTED COUNT	
		Total	Toads per Acre		Total	Toads per Acre
7/51-9/51.....	67.6	36	261.4	192.2	97	546.8
10/51-1/52.....	74.2	46	334.0	187.9	132	621.6
3/52-5/52.....	44.6	40	290.4	178.2	127	598.0
6/52-8/52.....	26.2	38	275.9	84.4	120	565.1
9/52-12/52.....	55.7	49	355.7	148.4	130	612.2
1/53-3/53.....	49.2	38	275.9	129.5	130	612.2
4/53-6/53.....	25.6	31	225.1	93.4	97	456.8
6/13-30/53.....	28.3	32	232.3	85.4	92	433.2
7/53.....	13.7	36	261.4	49.7	47	221.3
8/53.....	17.8 ¹	27	196.0	58.4	78	367.3

Data from plot 1, in Tables 14 and 15, show that in general there was a gradual decrease in density from the beginning to the end of the study. This continued decrease reflected the lack of any really successful reproduction during the research.

NATALITY

REPRODUCTION

Spadefoot toads (*S. holbrooki*) do not have a particular breeding season in the cyclical, seasonal sense, but rather breed only during or after very heavy rainfall. They reproduce in temporary water, and their loud, harsh voices elicit movements to the breeding areas. Bragg (1945) cited the above observations as characteristic of the xeric amphibian breeding pattern. He further pointed out that spadefoots fall into two general groups with respect to breeding response. One group responds to violent rainstorms while *S. huerteri* and *S. holbrooki* are greatly stimulated by large amounts, but not violence, of rainstorms.

Dr. C. J. and Mrs. Olive Goin have recorded the dates of spadefoot reproduction in a temporary pond in their backyard near Gainesville on: September 24, 1947, a large chorus after a storm; March 9, 1948, breeding chorus; April 5, 1949, a large chorus after rainstorms; August 22, 1949, a heavy rain and another chorus; September 5, 1950, a very heavy breeding group after hurricane rains; and October 18, 1950, breeding at some distance from Goin's residence after another hurricane.

The first chorus recorded during this study was associated with a passing cold front that brought 2.18

in. of rain during the night of September 17, 1951. Not many more than a half dozen pairs bred in Goin's backyard and none were recorded near the Drug Gardens, nor near plot 1. A small chorus after a heavy thunderstorm near Micanopy was reported by Dr. Archie Carr on September 22, 1951, but no spadefoots were known to have bred around Gainesville. The production of young from the former chorus was negligible.

A stationary cold front brought steady, heavy rainfall beginning on February 15, 1952; 3.14 in. were recorded on the University campus the morning of February 16, and 0.84 in. the next morning. They bred the night of February 15, in the Goin's backyard, and near plot 2. Cold weather followed, with minimum-maximum temperatures (F) reported on February 16 as 55-70°; 17, 37-62°; 18, 41-68°; 19, 47-75°; 20, 57-74°; 21, 48-72°. The water temperature at noon on February 19, in the breeding pond at Goin's was 55° F. The eggs began to hatch on February 21; the incubation time was 6 days. No young produced in this chorus were observed in the plots.

Large breeding congresses the early morning of April 7, 1953, were associated with a cold front that gave Gainesville 4.58 in. of rain for the day. Toads were not calling at 10 p.m. the night before, but Mrs. Goin heard them calling at 3:30 a.m., and they were still breeding at 7 a.m. They also bred north of Gainesville and in plot 1. Eggs were found in seven shallow (less than 18 in. deep) puddles in the grass prairie between plot 1 and Hogtown Creek to the north, the closest to the plot being: 1, 50 ft. north-east A-1, 2, 65 ft. north-northeast A-1, and 3, 200 ft. north D-1. A number of breeding ponds in the hammock south of plot 1 contained eggs with the closest being 300 ft. southwest C-1.

A barometric recording begun at 2 p.m. on April 7 showed a low of 29.6 in. at that time with a steady rise to 29.84 at noon the following day. Some toads were calling the night of April 7, but in the ponds only several pairs in amplexus were discovered. Many males but no unpaired females were observed. The eggs had hatched by 8 p.m. on April 8, an incubation period of less than a day and a half.

None of these ponds around plot 1 retained water long enough for the tadpoles to metamorphose. The puddles in the prairie were dry by April 25, and the pond 300 ft. southwest of C-1 was reduced to a puddle 1 in. deep and several feet in diameter by April 30. Some rain gave respite, but by May 3, the pond was dry and the tadpoles had not yet emerged. Very few young were produced from this reproductive period.

Another stationary cold front brought heavy, continued rains that stimulated large choruses in the Gainesville region on August 23, 1953. Toads began calling in mid-afternoon and continued in breeding choruses all night. Recorded daily rainfall beginning August 21 was 0.21, 1.66, 0.74, 2.60, 0.41, and 1.25 in. The eggs laid in this period were hatching by mid-afternoon, August 24, the hatching period being about

24 hr. or less. This chorus was large and a considerable population of young toads emerged after the present study was concluded.

All four records of breeding were associated with long, heavy rainfall during frontal weather. Time required for eggs to hatch varied from about one day in August, 1953, to six days during colder weather in February, 1952. For a detailed description of larval stages, reference should be made to Trowbridge (1941, 1942) and Richmond (1947). No observations were obtained on the behavior, mortality, or other factors during the time of movements of the young away from the ponds. Young toads were seen the afternoon of September 27, 1953, apparently heading in all directions from several ponds. Records kept by the Goins indicate that about six weeks elapse between emergence from the pond and initiation of burrow life. Recently emerged young were observed on June 2, 1949, and most of them had disappeared and had probably burrowed by the end of July, 1949. Many small young appeared from the ponds September 18, 1949, and most had utilized burrows by the last of October. Young emerged on October 1, 1950, and began to burrow by October 29, with nearly the entire group disappearing by November 16, 1950.

GROWTH

Measurements of growth were limited to determining the greatest head width, interorbital distance, and snout-vent length. Weights were not observed. The interorbital distance was measured with vernier calipers only through October, 1951, since difficulty was met in establishing definite landmarks for reference. Body length was not easily taken since the toad could contract or relax and thus change its size. Head width provided the most constant, least variable, and most used body measurement. Data for October, 1951, for plot 1 illustrate the relationships between these three body sizes. If Y = head width, X = body length, and Z = interorbital distance, the relationships are expressed by: $Y = 3.63 + 0.269X$; $Y = 15.28 + 0.293Z$; $X = 0.923 + 0.0917Z$.

The age of only a few individuals was definitely obtained in the study of growth rates. They were produced in the September, 1951, breeding and the records of their growth are given through the first 18 months in Table 16. To examine rate of body growth in plot 1, individuals captured for the first time between July and September, 1951, and later retaken at least once, were placed in categories according to their first observed head width. Only one measurement per individual per month was utilized in this work.

The type of growth illustrated by young from the September, 1951, reproduction was that of very rapid growth in the first few months with the rate of change decreasing as head width increased. These early data were better described by the curvilinear equation $Y = 8.4 + X^{0.21}$, than by the first degree equations in Table 16. Likewise for the group beginning at 14-15 mm the equation $Y = 13.91 + X^{0.065}$ more

TABLE 16. A summary of head width growth data from plot 1 with the appropriate values to be substituted in the equation $Y = Ay + bX$ where Y is head width in millimeters and X is time measured in months. F values with ** are at or beyond 1% level of significance.

Data Source	Number Toads	Number of Records	Ay	b.	F.
Age					
0-6 mo.'s.....	11	11	6.40	$1.212 \pm .0639$	39.9**
7-12 mo.'s.....	8	14	8.76	$0.474 \pm .0405$	11.3**
13-18 mo.'s.....	8	17	12.23	$0.165 \pm .0355$	1.44
Size					
14-15 mm.....	31	158	14.70	$0.101 \pm .0007$	145.00**
16 mm.....	23	158	16.07	$0.056 \pm .0005$	63.78**
17 mm.....	61	252	17.02	$0.049 \pm .0003$	89.18**
18-19 mm.....	41	192	18.48	$0.023 \pm .0005$	12.38**
20+ mm.....	8	42	20.21	$0.017 \pm .0027$	0.95
14-15 mm.♂.....	10	59	14.40	$0.124 \pm .0128$	93.10**
14-15 mm.♀.....	13	80	15.16	$0.077 \pm .0119$	42.10**
16-17 mm.♂.....	19	132	16.42	$0.107 \pm .0045$	561.00**
16-17 mm.♀.....	41	275	16.54	$0.041 \pm .0053$	60.10**
18-19 mm.♂.....	26	103	18.35	$0.047 \pm .0088$	28.53**
18-19 mm.♀.....	15	89	18.17	$0.040 \pm .0084$	22.40**

nearly described the observed data. In the larger size groups a rectilinear equation (Table 16) expressed the records satisfactorily.

An examination of records of toads first reported as juveniles showed that on the average they attained sexual maturity during their second year after metamorphosis. The average head width of 47 female toads when their sex was first detected by the presence of ovarian eggs was 15.36 mm. The average head width of 32 males when the dark epidermal pads on the fore feet were first seen was 15.70 mm. The actual size of adult attainment was possibly smaller than these averages, since time probably elapsed between development of the sex characteristic and its observation. Head widths such as these were reached on the average at 19 and 15 months respectively.

An analysis of sexual divergence in growth rate was made for toads that had an initial head width of less than 13.0 mm, that were first observed between July and September, 1951, and that reached sexual maturity during the period of study. Forty-one records involving 7 males are expressed by the equation $Y = 11.81 + X^{0.125}$, and the average size two years later was 17.55 mm. Eight females were recorded 47 times and the equation $Y = 11.74 + X^{0.103}$ produced the average Y value 16.22 mm when X was 24 months.

For a comparison of male and female growth rates in the larger size groups rectilinear equations were used and the data are presented in Table 16. Using the null hypothesis a test (t) was made for the significance of difference between the rates of growth or regression coefficients (b) for the two sexes. In the category 14-15 mm the males grew at a faster rate (coefficient b larger) than the females and the difference was significant at the 1% level ($t = 2.67$). In the 16-17 mm group the males still grew faster than the females ($t = 9.47$, $P < 0.01$). In the largest

size category, the rate of growth for both sexes was less than for the smaller toads, but in these older ones the rate of growth for the males was only slightly larger than that of the females and the difference lacked statistical significance ($t = 0.4$).

To represent growth data on the 494 individuals from plot 1 that were taken two or more times is not feasible because of the space that would be required. However, two males and two females were chosen for each of the beginning head width categories (except the largest one) on the basis of those with the largest number of captures over the longest period of time. The records of these individuals are given in Fig. 9.

One of the objectives of work in plot 3 was to determine the effect of density on rate of growth. Records were plotted so that three major sources of variation could be analyzed; the sources were: (1) effect of differing initial body sizes, (2) a seasonal or temporal effect, and (3) population density. Three categories of beginning head widths were erected that were: (1) 12 and less, (2) 13-14, and (3) greater than 14 mm. The study extended from June, 1952 through November, 1953, and these three periods of 6 months' duration were chosen: (1) June through November, 1952, (2) December, 1952, through May, 1953, and (3) June through November, 1953. The three density levels were discussed earlier. The data were tabulated so that, if necessary, the results for a particular time, under one density, and in a certain size group could be studied.

Analyses of covariance indicated that there was significant variation between size categories only for the first 6 months period where the smallest toads were growing at a faster rate than others. This rapid growth of the small toads during the first 6 months was probably responsible for the significant variation between the 3 time periods, as there was no real difference between rates of growth for the second and third periods.

Using data from all size groups for the entire study an analysis of covariance disclosed that a statistically significant variation existed between growth rates in the three density levels ($F = 37.6$, $P < 0.01$). The average mm increases (b) per month under the high, medium and low populations were respectively, 0.0901 ± 0.0311 , 0.1614 ± 0.0290 , and 0.2233 ± 0.0460 . The highest density had the lowest rate of growth. Using the null hypothesis in a test for significant differences in regression coefficients or growth rates the difference between high and middle densities was not significant ($t = 1.7$, $P = 0.10$) and neither was that between middle and low ($t = 1.1$), but the difference between high and low levels was significant at the 2% level ($t = 2.4$).

Another test of density effects was restricted to the first 6 months of study and the data were further subdivided into size groups. An analysis of covariance of the 12 mm and less size group disclosed significantly greater variation between density levels than within them ($F = 6.9$, d.f. = 36, 2, $P < 0.01$). The regression slopes for the high, middle, and low densi-

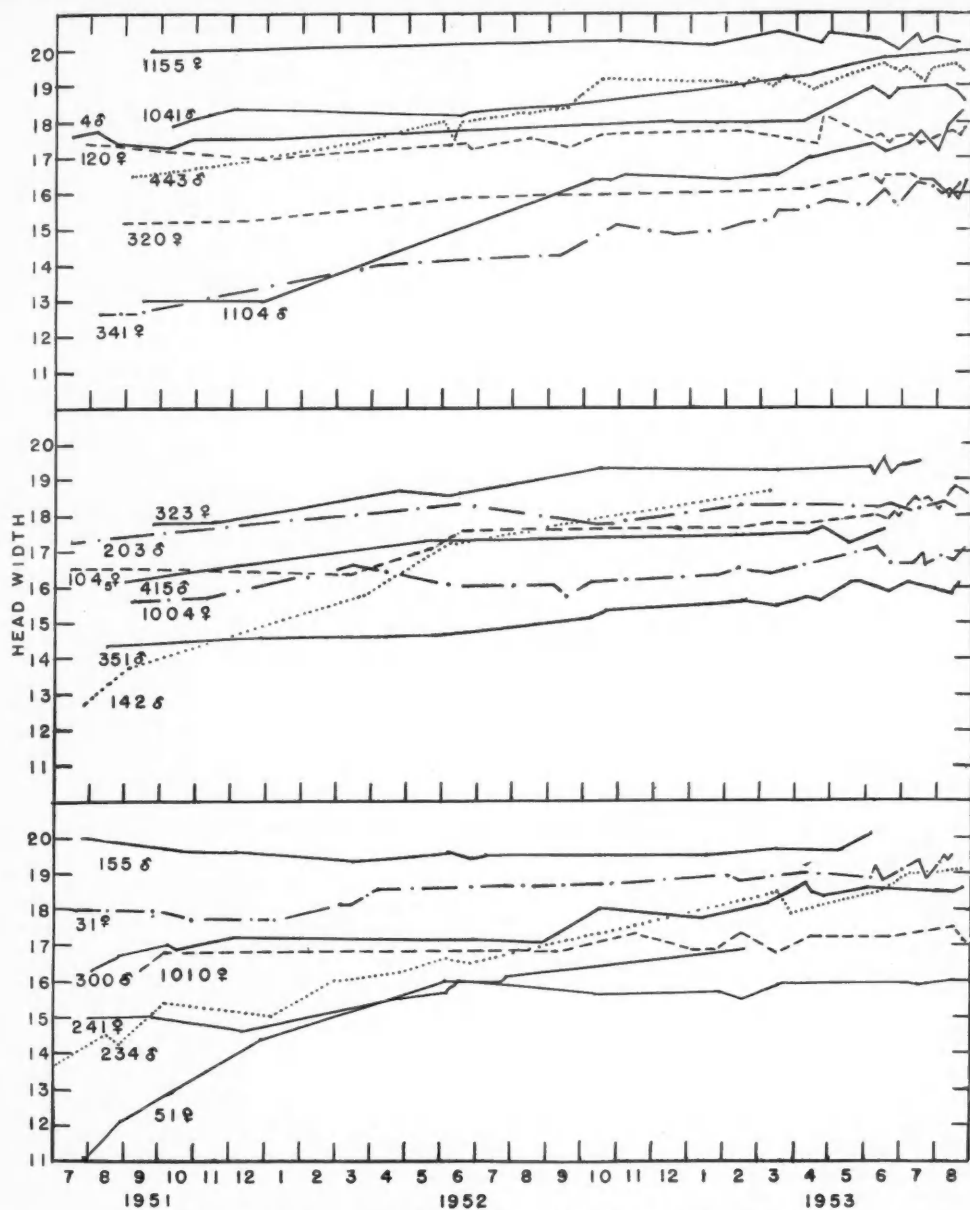


FIG. 9. Records of head width growth for 11 male and 11 female toads.

ties were 0.1959 ± 0.1950 , 0.8323 ± 0.0995 , and 0.9002 ± 0.2250 . The probability that differences as great as those observed in these growth rates could be obtained by chance alone is 0.005, 0.05, and 0.02 respectively between the first two, the last two, and the first and last values.

Similar tests were made on the size group 13-14 mm head width and the F value from analysis of covariance was 3.69, which is at the 5% probability level.

The rates of growth for the high, middle, and low densities were 0.0907 ± 0.0707 , 0.1317 ± 0.0690 , and 0.4094 ± 0.1390 . Only in a comparison of the high and low density levels was a significant difference found between growth rates. This same series of checks was made on the data from the largest size category (greater than 14 mm) and greater variation was found between density levels than within them ($F = 4.36$, $P = 0.05$). The regression slopes were

0.0729 ± 0.387 , 0.2183 ± 0.0539 , and 0.3235 ± 0.0307 . The significance of difference in growth rates (b) was at the 5% level for the first two and at 0.025 when the highest and lowest densities are compared; however, no real difference was found between the low and middle density growth values.

To summarize, when compared with each other, the middle and low densities had no different effect on rate of body increase. In all of the tests a significant difference in rate of growth was shown between the highest and lowest population levels, and this was also true between the highest and middle levels for the sizes 12 and less and greater than 14 mm during the first six months of study. In all of the calculations, the rate varied indirectly with the population size.

The construction of a theoretical average growth curve for most of the toad's life was of value in age group distribution studies. Data from toads known to have been produced during the September, 1951, and April, 1954, breeding periods in plot 1 were combined to calculate the average head width for the first 24 months after metamorphosis. Concerning all of the data following this first period, an assumption was necessary for the age of the toads.

It was assumed for the purpose of these studies that if it took, for example, 5.2 months for these toads of known age to reach a mean head width of 11.81 mm, it would also on the average have taken the same time for toads from any other reproductive chorus. This assumption postulates equally favorable growth conditions. Therefore, for the males of the beginning category of 13 mm or less, the equation given above would fit a curve that joined the curve of the toads of known age and would extend to 31.2 months age. Using this assumption, curves for the categories 16-17 and 18-19 mm (Table 16) head width were added and the curve is given in Fig. 10.

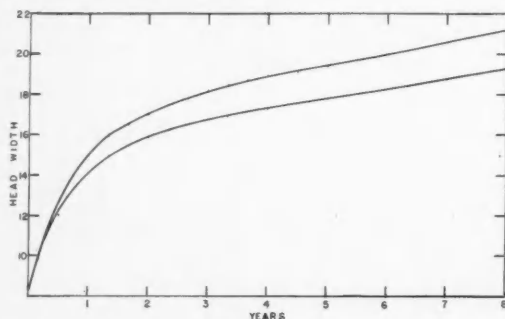


FIG. 10. A theoretical growth curve extrapolated statistically and combining growth rates for several groups of toads. The upper curve is for males and the lower represents female growth.

The same assumption was also made for female growth data. Categories of head width 13 and less, 16-17, and 18-19 mm (Table 16) were used to estimate the mean growth rate for females through eight years. These data are also illustrated in Fig. 10.

AGE GROUP DISTRIBUTION

The frequency distributions of head width in plot 1 were tallied for males, females, and for those of undetermined sex and these data are presented in Tables 17 and 18. If an individual was captured more than once in a month it was represented in the tally by only one measurement expressing the average for the month. The monthly frequencies were then lumped to form 9 categories of 3 months each.

The age group distribution of the population in plot 1 was estimated by making use of the calculated average growth curve in Fig. 10. It was recognized that any attempt to assign age to head width cohorts based on the average growth of the population was subjected to error caused by individuals attaining size ahead or behind the average. In this study, it was assumed that males were less than 2, 2-5, 6-8, or 9 or more years old if their head width was 17 and less, 18-19, 20-21, or 22 mm and greater, respectively. Likewise it was assumed that females and those of undetermined sex were, respectively, less than 2 yrs., 3-5, 6-8, or 9 or more years old if the head width was 15 and less, 16-17, 18-19, and 20 mm and larger. Using these arbitrary categories, the percentage age distribution was calculated.

TABLE 17. Frequency distributions of head widths given for males.

Head Width mm.	7-8 1951	9-11 1951	12/51-2/1952	3-5 1952	6-8 1952	9-11 1952	12/52-2/1953	3-5 1953	6-8 1953
11.....	2
12.....	1
13.....	3	3	2	3	1
14.....	3	4	3	7	2	2	..	1	..
15.....	4	14	7	7	5	4	4	1	1
16.....	5	9	8	10	16	5	8	8	6
17.....	17	21	13	16	23	27	21	22	36
18.....	18	26	13	19	24	31	27	35	31
19.....	11	20	10	12	11	18	25	48	34
20.....	5	12	2	7	13	15	5	6	29
21.....	..	2	..	5	5	4	..	3	11
22.....	..	1	..	1	1	4	3	4	..
23.....	1
24.....	1	1
25.....	1	1
Total...	70	112	58	87	101	110	93	30	150

Calculation of these percentages and careful study of head width frequencies indicate that the percentage of toads less than 2 years old dropped from 50% during the first period to about 22% during the last time period. The off-spring produced in connection with the breeding choruses of September, 1951, scarcely affected the total picture of age distribution and there was no evidence of young individuals from reproduction in February, 1952. The very small toads that appeared resulted from the preceding April breeding and represented only 6.7% of the population caught during the last time period in August, 1953. This small addition to the population after a reproduction as heavy as that of April, 1953, re-

TABLE 18. Frequency distributions of head widths given for females and those of undetermined sex in ().

Head Width mm.	7-8 1951	9-11 1951	12-51-2/52	3-5 1952	6-8 1952	9-11 1952	12-52-2/53	3-5 1953	6-8 1953
8.....	(4)
9.....	(1)
10.....	(1)	...	(1)	(1)
11.....	1 (3)	1 (1)	(1)
12.....	6 (5)	(1)	...	(1)	(3)	(2)
13.....	7 (8)	4 (8)	(3)	1 (1)	(1)	1
14.....	4 (8)	8 (12)	2 (9)	7 (3)	7 (7)	6	4 (5)	2 (2)	(4)
15.....	6 (2)	5 (11)	12 (7)	4 (6)	9 (1)	10 (3)	13 (3)	8 (1)	15 (1)
16.....	8 (1)	28 (6)	11 (3)	27 (5)	16 (2)	21 (2)	28 (5)	29 (2)	31 (1)
17.....	22 (2)	34 (3)	14 (2)	45 (3)	27	29 (1)	34	38	36
18.....	11	33	14	25	24	26 (1)	26	37	44
19.....	6	15	4	10	8	13 (2)	12	22 (1)	29 (1)
20.....	3	5	...	2	4	6	5	4	10
21.....	...	1	1	...	2	1	1	2	1
22.....	1	3	3	1	4	...
23.....	1	1	2	1
Total..	74 (30)	134 (42)	58 (26)	122 (19)	100 (14)	117 (9)	125 (13)	148 (6)	167 (15)

flected the very high mortality of larvae resulting when most of the ponds dried before metamorphosis.

The relative number of individuals in the 6-8 yr. class increased considerably from 12.6% at the first of the study to 34.3% at the end. The 9+ yr. class increased from 2.3% to a value of 4.2% through the study. Thus it is seen that the relative number of young toads decreased and the relative number of old toads increased through the duration of observation.

SURVIVAL AND DISAPPEARANCE RATES

Data on survival and rate of disappearance were selected by using only those individuals from plot 1 that were first observed between July and September, 1951, and only those that were resident in parts of the plots surveyed in 10 ft. quadrats. This selection provided records on a cohort that was under greatest field observation for the longest time. There were 153 toads recorded during these first 3 months.

Two major reasons for disappearance, other than death, were known. The toads could have simply moved from the area under consideration, or their periods of surface activity could have been such that they would not have been seen. With regard to the first point, a number that were first captured in the limited area under consideration were later retaken in adjacent habitats, so that possibly a large number of the cases of loss resulting from dispersal was prevented by the examination of these adjacent areas. A part of the apparent departure in the later part of the study was unreal and actually resulted from a lack of observation of these toads. If field work had continued, the number of toads surviving during the spring and summer of 1953 would have been recorded as much higher than that given in Table 19.

No records of actual death were obtained, but injuries were observed. Five toads had one entire front arm missing and two had most of one rear foot gone.

Death from fire is a possibility. In plot 1 a campfire at D-5 (Fig. 1) between October 25 and 28, 1951, apparently caused burns over most of the venter and one forearm of a female, for on November 13, 1951, the healing wounds were seen when it was caught at 4 NE F-3. The burns eventually healed and the toad survived throughout the study.

The records of percentage apparent survival in the plot 1 cohort as well as data on these toads grouped into 3 size categories are given in Table 19. A large drop in survival percentage occurred during the first several periods, and disappearance was high during the September, 1951, and February, 1952, breeding seasons. The rate of loss between April, 1952, and March, 1953, averaged 6 toads per 100 for each 3 months.

With regard to survival in the 3 size groups the lowest rate was for the smallest toads, and the largest toads also had a low survival value while the 15-17 mm category had the highest rate of survival (Table 19). No significant difference in apparent survival existed between the sexes; the percentage survival of 53 males was 62.3, while that for 68 females was 63.2 through March, 1953. The average disappearance rate through this period was 7.54 per 100 for males and 7.21 for females per 3 months.

TABLE 19. A summary of survival and disappearance rates for a selected cohort from plot 1.

Time Unit	TOTALS		14 MM. AND LESS		15 TO 17 MM.		18 MM. AND GREATER	
	% Survival	Rate of Loss	% Survival	Rate of Loss	% Survival	Rate of Loss	% Survival	Rate of Loss
10-12/1951.....	79.7	25.4	75.0	25.0	79.2	20.8	82.1	17.9
1-3/1952.....	71.2	10.7	64.6	13.9	75.3	4.9	71.4	13.0
4-6.....	67.3	5.5	54.2	16.1	72.7	3.5	71.4	0.0
7-9.....	62.8	6.8	50.0	7.7	68.8	5.4	67.9	5.0
10-12.....	58.8	6.3	45.8	8.3	66.2	3.8	60.7	10.5
1-3/1953.....	55.6	5.6	45.8	0.0	61.0	7.8	53.6	11.8
4-6.....	40.5	27.1	31.3	31.8	45.5	25.5	42.9	20.0
7-8.....	27.5	32.3	22.9	26.7	27.3	40.0	35.7	16.7
Average through 3/53.....	10.0	11.8	7.7	9.7

The density effect on survival was studied in plot 3. Since the fences prevented emigration-immigration of toads, the disappearance in this plot more certainly reflects actual death than in the unfenced one. The highest survival values were in the medium densities, while much lower values were shown in the high and low population levels. Likewise the highest average rates of loss, 6.30 and 5.83, were found in the high and low levels, while the average, 4.11, in the medium populations was the lowest (Table 20). The rates were based on monthly time units. If the data were recorded in three-month periods for plot 3, the average disappearance rates were 24.7, 12.7, and 17.6 per 100 for the high, middle, and low density levels, respectively. The average rate for all data from plot 3 through March, 1953, was 15.14 whereas that for plot 1 was 10.03.

A seasonal variation in disappearance rate was ob-

TABLE 20. A summary of survival and disappearance data from plot 3.

Time Unit	HIGH DENSITY		MEDIUM DENSITY		LOW DENSITY		TOTALS	
	% Survival	Rate of Loss	% Survival	Rate of Loss	% Survival	Rate of Loss	% Survival	Rate of Loss
1952								
7.....	92.5	7.5	92.5	7.5	75.0	25.0	89.0	11.0
8.....	77.5	16.2	87.5	5.4	75.0	0.0	81.0	9.0
9.....	70.0	9.7	82.5	5.7	75.0	0.0	76.0	6.2
10.....	70.0	0.0	82.5	0.0	75.0	0.0	76.0	0.0
11.....	70.0	0.0	80.0	3.0	75.0	0.0	75.0	1.3
12.....	67.5	0.0	80.0	0.0	75.0	0.0	74.0	1.3
1953								
1.....	67.5	0.0	80.0	0.0	75.0	0.0	74.0	0.0
2.....	67.5	0.0	77.5	3.1	75.0	0.0	73.0	1.4
3.....	65.0	3.6	75.0	3.2	75.0	0.0	71.0	2.7
4.....	57.5	11.5	72.5	3.3	65.0	13.3	65.0	8.5
5.....	52.5	8.7	70.0	3.5	60.0	7.7	61.0	0.0
6.....	45.0	14.3	62.5	10.7	55.0	8.3	54.0	11.5
7.....	37.5	16.7	55.0	12.0	40.0	27.3	45.0	16.7
8.....	37.5	0.0	55.0	0.0	40.0	0.0	45.0	0.0
9.....	20.0	46.7	50.0	9.1	35.0	12.5	35.0	22.2
10.....	20.0	0.0	42.5	15.0	35.0	0.0	32.0	8.6
11.....	20.0	0.0	35.0	17.7	25.0	28.6	27.0	15.6
Average through 8/53.....	6.3	4.1	5.8	15.1

served in plot 3 and is recorded in Table 20. The highest average values from July, 1952, through August, 1953, were for July and August, 1952, and next highest for June through August, 1953, the three-month average values being respectively 10.3 and 9.9 losses per 100 toads per month. The average of monthly rates were 2.1, 0.4, and 4.8 for September-November, 1952; December-February, 1953; and March-May, respectively. For these periods, highest apparent survival rates occurred when the activity rate was low during the winter months of 1952-1953. The rates of loss were high during the fall of 1953, but since this was the end of the study, many of the toads not recorded would probably have been caught if work had continued.

DISCUSSION

The common name of hermit or solitary spadefoot toad for *Scaphiopus holbrooki* probably arose from the many reports of its secretive underground life. A number of writers have shown interest in the secretive behavior, and Wright (1932) summarizes the most important of these. The author gets the feeling, in reading some of these descriptions, that the early observers viewed with a mystical awe the sudden deluge of breeding toads after a heavy rainfall; especially when they were considered very rare between choruses. Bragg (1944) refuted the idea that spadefoots seldom emerge from underground burrows. Concerning this idea it was found that toads emerged from their burrows about 8% of nights on a long-term basis and remained definitely underground at least 58% of the time, and probably much more. The number of days spent underground without emergence varied from one to 104, and averaged a little under 10 days. The time underground was associated

with the winter and summer months. The number of emergences from marked burrows during the spring and fall seasons was significantly greater than that of the other seasons; the increased emergence was especially apparent during March and April and September and October. This increase in these seasons may be associated with (1) a greater amount of optimal activity weather than occurs in winter or summer, or (2) a greater food supply available during the spring and fall than in the other seasons. Given suitable climate, the individual toads may be just as active one part of the year as during another. A precise cyclical type of hibernation-aestivation was not illustrated. Seasonal factors likewise affected the distance of movement from a known burrow in feeding operations.

Phylogenetic interpretations based on habits (Bragg 1945) and on morphology (Tanner 1939) have indicated that the center of origin of Scaphiopodidae was near northern Mexico. It was concluded by these authors that this xeric form divided into two lines, one of which was the subgenus *Scaphiopus* including *S. holbrooki*, that moved into mesic conditions of eastern North America. Bragg (*ibid.*) observed habits, especially those related to breeding patterns, that indicated a phylogenetic link with forms having xeric adaptations. He further concluded that the subgenus that moved east has adapted to a mesic environment in many respects. The toads inhabited forested areas in this study with the largest populations in the more mesic hammocks and in the ecotone where soil moisture was high; the statistical analyses indicated that they were more active during moist, mild weather. Rainfall and atmospheric moisture are major factors influencing spadefoot activity; the highest coefficients of correlation were obtained between the number of toads observed per unit time and the amount of daily rainfall. Significant correlations were also found between activity and air moisture, but for other factors the data had to be lumped to show only a general association between weather and activity. Rainfall is more effective in this regard than atmospheric moisture, which, in turn, is more effective than temperature. These data substantiate for *S. holbrooki* a conclusion of Bragg (1944) for *S. bombifrons* that they tended to leave their burrows in greater numbers during and after rainfall than at dried periods, and that decreased activity during hot, dry summers was usual.

Concerning the time of nocturnal activity, Carr (1940) said: "On winter nights they emerge from their holes about eight-thirty or nine o'clock; even in an area thickly populated with spadefoots it is very unusual to find one in the open before eight p.m." Data from the present study indicated that a peak activity occurs immediately after sundown with a smaller peak just before sunrise; whereas the lowest activity occurs about 2 a.m. The time of these peaks varies with the time of sunrise and sunset. During nights when work was done at sunset, before dawn, or through the entire night, it was seen that the increase in toad activity coincided with quickening of

other life. The calls and movements of birds were noted, but the nuisance of mosquitoes was most striking about the time toads became more active before dawn. Park (1940) discussed the general problem of nocturnal activity and cited literature illustrating that the community is divided into species characteristically nocturnal and those normally diurnal. Park, Barden, & Williams (1940) gave an illustration representing activity of nocturnal and diurnal species at sunset, from which I conclude that in a general way the total number of species active may be greater in the period of gradual overlap of day and night.

Time of spadefoot activity may be correlated with physical factors since temperature and vapor pressure deficit decrease relatively fast during the early evening and toads may well be stimulated by this. However, temperature and humidity vary only slightly, and for practical purposes none, in the hour before sunrise. This would seem to eliminate correlation with these factors for the pre-dawn increase in activity. It is possible that this high toad activity rate in early evening and morning is an adaptation to optimal times for food capture. The overlap of day and nighttime brings a mixture of prey that are typically nocturnal or diurnal, and analogy to the interdigitation of species in the ecotone between two communities might be made, i.e., a kind of a temporal ecotone.

The type of behavior, with regard to emergence from burrows, offered a serious drawback to the estimation of population densities by index methods. The data presented in this study indicate that there is a rotation of utilization of toad-habitat by segments of the total population. One part appeared night after night for awhile and then remained inactive for a second unit of time. It would appear for several days and feed and then remain underground for a considerably longer period. The active and inactive cohorts were not discrete, but rather the individuals composing the groups changed continuously; in fact, during optimal weather all or nearly all of the group may emerge. It is possible that this behavior was related from a phylogenetic standpoint to the adaptations of desert forms to longer periods of subminimal environment and only brief intervals of optimal weather. This type of response might be necessary in a xeric community, but would not necessarily be detrimental in a mesic one.

If the situation described above is true, the index methods of population estimation would not measure total toad population size, but rather estimate the segment that was active. The index methods did underestimate the population, especially during minimal toad weather during the summer periods. The explanation probably lies in the necessary assumption for the index methods that the released animals mix at random with the total population. This was negated for *Scaphiopus* since there was evidence that toads did not emerge from their burrows at random with regard to time, and the inactive percentage appeared to be larger during some seasons than at others. The

Tanaka index would not adjust for this source of error, since in this case the probability of observation was not a function of whether the animal was marked or unmarked. Rather it was (1) a function of environmental suitability for toad activity and (2) the amount of time the individual had already been active before it was observed for the first time in a census period. For if it had already emerged for several nights it might not be as active during the census period as it would if it had been underground for several weeks or months.

Travels for the possible collection of food away from a known burrow were significantly greater in the ecotone than in the hammock. Likewise, and as a direct result of the greater movements, the home ranges of toads in the ecotone were greater than those in the hammock. The spatial distribution of capture sites in the hammock was random. However, in the ecotone while the burrows were spatially at random, there was good evidence that the toads aggregated in their feeding operations. This grouping from spatially random burrows would require greater movements than, for example, in the hammock where the burrows and capture sites were distributed alike. The areas of aggregation in the ecotone were in the open habitat near the junction with herbaceous growths of the prairie grasses. Another area of toad concentration was around large piles of leaves, twigs, and rotting plant materials. Probably the movements of toads were in response to optimal food conditions.

These data were analyzed using ten foot quadrats. When data from the same area were tested, using 25 ft. sample plots, a contagious distribution was illustrated (Cole 1946): In this case the toad distribution seemed to be correlated with the type of micro-habitat. Cole (*ibid.*) hypothesized that contagious distributions may be made up of intermingled random distributions of groups of different sizes. Data from the present study may substantiate this, since when the contagious distributions of the larger sample plots were restudied using smaller quadrats, random distributions were indicated in all except the ecotonal capture-site records.

The analysis of food habits by studying four collections of stomachs in each of the seasons produced results that do not differ greatly from those of Carr (1940). The percentage composition of total bulk in his study was: Gastropoda, 2.3; Myriapoda, 25.6; Lepidoptera, 11.6; Orthoptera, 27.9; Arachnida, 9.3; Coleoptera, 18.6; vegetable, 2.3; unidentified and sand, 2.3. Bragg (1944) reported that he had no record of *Scaphiopus* eating vertebrates, but he did have record of their eating spiders, flies, hymenoptera, moths, beetles, and bugs.

Smaller toads had a significant tendency to move greater distances than larger ones in feeding. There is probably an obvious connection between this and the calculated higher rate of loss for small toads than for larger ones. The greater the distance a toad moves from its burrow, the greater the probable chance of capture. In addition to these hazards con-

needed with distance the toad is likely to be less well orientated with regard to escape.

An examination of burrow and capture sites for toads living where the forest micro-habitat with little or no vegetation in the lower strata meets the prairie habitat with its densely vegetated cover, indicated that they almost always moved from their burrows to the more open areas. Their holes were so situated that movement in one direction would have carried them into dense, low plant growth and in the other into open forest areas. The observed behavior may possibly reflect the phylogenetic connections this species holds with desert forms illustrating a similar functional response to prairie or open habitats through adaptation or preadaptation.

The variability in home range size was tremendous. The large variation produced parameters that made reaching statistically significant conclusions very difficult. Differences were shown, however, between range-size for toads having only one burrow as contrasted with those having more. Significant correlations were also shown between range-size and number of captures per individual.

Data suggested that spadefoot toads have several burrows within their home range that are occupied alternately. Nest movement within a home range was reported for mammals by Nicholson (1941), and for birds by Erickson (1938). This is the first record of burrow or home-site movement within a home range for amphibians, and also the first record of an alternating use of nest sites within a home range. In estimating home range size, one must consider not only the length of time involved in the study, but also the relationship of burrows or nests to the range. If a study was of such short duration that only wanderings around one of several burrows were recorded, the size of the true range would be considerably underestimated by the observer.

A statistical treatment of capture data was devised by Hayne (1949 a) to locate the geographic center of activity that he used in a method of home range size estimation. Such a center of activity was calculated for one toad in this study, #3241, indicated by a + in Fig. 6, to show its relationship with the biological center of activity, the burrow. If certain toads had been chosen, i.e. #1305 in Fig. 6, or #3040 or #1033 in Fig. 5, the statistical center would have been further distance from the burrow. This adds evidence to Hayne's statement that the center of activity does not necessarily have any biological significance apart from being an average of capture points.

In a review of the literature of range analysis, Hayne (*ibid.*) discussed one method where it was assumed that the greatest distance between points of capture constitutes the diameter of a circle, or major axis of an ellipse, which is the animal's home range. For this method then it is assumed that home range shape is that of an ellipse or a circle. Enumeration of home range shape frequencies for the spadefoot illustrated that the majority were not circular or elliptical in outline, and the assumption of such a shape would not be correct. Data from the home range studies fur-

ther substantiated Dice's (1952) conclusion that in many cases, the location of the burrow is not central to the home range.

The relationship between the concept of home range and territoriality needs consideration. Any animal consistently occurring in a particular area might be said to have a home range. If other members of the same species, and more specifically members of the same sex, are excluded from the area, the concept of territoriality is illustrated. The difference in the concept used depends on the definition used by the observer for territoriality and on his skill in observation.

Territoriality has been reported for many species of birds and mammals. One definition often used, especially for birds, is that territoriality involves the defense of a specific area either by physical contact and/or by threat display. No threat, combat, or any kind of aggressive display was observed in this study. It may be that only those species with more obtrusive behavior are known to conform to this definition while the phenomenon might actually exist in some species in which the defensive fighting or display is too subtle for the observer to discern. Recently, one type of territoriality in breeding amphibians was shown by Martoff (1953), using statistical means to illustrate that breeding *Rana clamitans* maintained relative positions. Dice (*op. cit.*) uses a similar idea in stating that if individuals of the same sex have ranges that do not overlap, it is generally assumed that territoriality exists. In the study of Scaphiopus ranges, when only 90% of captures for any given animal were utilized, the overlap was not great, and when the ranges were plotted separately for males and females, there was only very slight overlap. In the most crowded part of the plot, the overlap was slight when plotted for the 26 months and did not exist between individuals when small time units were used. According to this definition, the spadefoots exhibit a territorial behavior.

Another definition is as follows: "Territoriality includes homing or the defense of a given area, or both. Homing reactions are concerned with an animal's becoming so adjusted to a specific area that returns are made, perhaps to the precise spot, when activities or environmental accidents cause removal" (Allee et al. 1949). Under this definition Breder (1927) would have documented the existence of territoriality in amphibians. He reported that *Rana clamitans* returned considerable distances to its home area, and he recorded homing movements as great as one-quarter mile in *Bufo fowleri*. Likewise, territoriality in amphibians would again be substantiated since the homing reaction was shown for spadefoots; some individuals returned over long distances from breeding choruses to their original site of departure. Griffin (1953) gave a general discussion of various types of orientation and mechanisms employed in homing behavior, some of which might be useful in a needed study of spadefoot orientation in homing migrations.

The combination of low rates of dispersal, the homing behavior, and territoriality may be quite important in the evolution of this species. The terri-

torial behavior tends to stabilize the population, and if the toad habitat were already occupied by individuals with established territories, new toads would be discouraged in immigration attempts. This behavior would reduce dispersal and mixture of the groups using different breeding ponds. Another isolating mechanism is the homing reaction that insures that a large proportion of toads leaving their home area and migrating to the pond would return to their home site. All seven of the plot 1 residents that were observed during breeding movements were later seen back in the plot. Further research is needed to test for possible genetic effects that might result from the semi-isolation of spadefoot populations by the territorial and homing behavior.

Dispersal from one breeding population to another occurs when some toads fail to return home from reproductive migrations. It also occurs when individuals move small, cumulative distances in one direction, taking them from one breeding population to another. The dispersal of young in all directions from the ponds probably continues until the young have found suitable habitats. If there is available space for addition of new members to the group, it seems reasonable to suspect that the young would establish themselves in areas nearest the pond. They would continue to move from the pond area if there were no available niches or if the habitat were unfavorable.

By the end of the study, the density of plot 1 was reduced to one-third of that beginning in July, 1951. The study of survival values indicated that the percentage remaining under observation was in this same order of magnitude. This cut in number resulted from poor reproductive success in the 26 months during which observations were made. Under some conditions this lack of successful reproduction could have continued, and since mortality continues, the population would become quite small. As the number decreased, the toad populations around particular breeding sites might become more isolated.

Population density in the ecotone was about double that in the hammock. The soils were wetter in the ecotone than in the hammock, and thus might provide more nearly optimal conditions. Probably the major factor was that in the ecotone there was a mixture of animal species characteristic of both the prairie and the hammock and the food supply would then be greater than in the hammock.

Two phenomena, (1) that the density of the spatial ecotone was about double that of the homogeneous habitat, and (2) that the observable surface activity during the early evening and predawn hours greatly exceeds that of the other nocturnal hours, may possibly be related to the greater food supply found in the tension zones or spatial or temporal ecotones.

During the first months of study the population density was high, and only about half of the toads were functionally adult. After 26 months of poor breeding success, the density was cut to one-third its original level, but the percentage of the population of reproductive age was very high. The age group

distribution had changed during the study from one with a large percentage of young to one in which only about 22% was less than two years old. This may be a type of self-regulating mechanism, whereby, as the density decreases, the percentage of functional adults increases.

Speaking of growth in the higher animals, Thompson (1948) said that "in all cases growth begins slowly; it attains maximum velocity somewhat early in its course, and afterward slows down towards a point where growth ceases altogether. But in cold-blooded animals, as fish or tortoises, the slowing down is greatly protracted, the size of the creature would seem never to reach, but only to approach asymptotically to a maximal limit." The growth curve illustrated for toads in this study did not follow the typical S shape, but rather began immediately with a very rapid rate of increase. The earlier unmeasured stages of newly emerged spadefoot growth may have illustrated the slow beginning rate. The measured rate decreased as growth continued, and the oldest individuals still had a slight but perceptible increment.

The dampening effect of overcrowded individuals on growth rate has been shown many times. (Allee 1951); the present study adds to the evidence for amphibians under natural conditions. These data illustrated that there was an inverse relationship between increased density and a decreased growth. The difference between growth under the highest and lowest levels tested was statistically significant as it also was in several tests between the highest and medium density levels. In none of these tests between growth in the lowest and medium levels was a real difference found. The reason for the decreased growth probably lies in the lesser food supply per individual. Also, with a larger group there is more mutual stimulation, thus increasing the amount of activity and amount of energy expended for functions other than growth (Ludwig & Boost 1939).

One big gap in the knowledge of *Scaphiopus* concerns its predators. The underground daylight existence and the nocturnal feeding operations reduce danger of capture as well as make it difficult to obtain predation data. Goin (1947) observed a hog-nosed snake (*Heterodon simus*) removing a spadefoot from its burrow while Carr (1940) reported the predation of toads in breeding chorus by several species of gulls in the streets of Tarpon Springs, Florida. McAtee (1932) did not list *Scaphiopus* as preyed on by Nearctic birds. During breeding periods of April and August, 1953, a sizeable quantity of eggs failed to develop, and leeches (Hirudinea) were seen in the egg masses. McAtee (*ibid.*) said: "Leeches prey upon eggs and young amphibians and there are numerous insects which destroy tadpoles, such as the giant water bug, backswimmers, water scorpions, predaceous diving beetles and their larvae, and the nymphs of dragonflies." In the larval stages it is probable that a large number are killed by predators and many die when ponds go dry. Childs (1953) reported nearly 75% loss of spadefoot tadpoles, possibly from preda-

tion by the raccoon (*Procyon lotor*), after 19 days of larval development. Only 50 individuals survived from a beginning population of 200 larvae in this experiment. When the young toads emerge and disperse, until satisfactory habitat conditions are found, it is believed that a large loss occurs as a result of predation and unfavorable physical environment.

In this study, the precise relationship is unknown between disappearance and death rate. In the non-experimental field plot, death, dispersal, or the failure to observe resident toads combined together to produce an effect equal to the disappearance rate. Since habitats around the selected area of mortality study were searched for toads, the fraction of losses resulting from dispersal was considerably reduced. A number of toads originally recorded in the area under consideration were later observed in adjacent areas. The disappearance data through March, 1953, probably does not include many individuals that were living in the area but were not seen, since nearly a third of the total field hours of observation in this plot were made after March. This should have been sufficient field time to reduce greatly the number of resident toads that were present but not captured. It is believed that the rate of loss of toads in plot 1 through March, 1953, closely approaches the actual death rate.

The approximation of death rates by disappearance rates in plot 3 was even closer, since the fences prevented dispersal of the population. Although the toads were examined when found outside enclosures, none was ever caught that had escaped from a pen. There was evidence during the latter part of the study that toads were immigrating into pen 3, but the reverse was not true. If loss data are restricted to those through August, 1953, so that ample observation hours followed to record the presence of toads inactive during previous months, they would represent death rates quite accurately.

In these experimental areas it was shown that loss was lowest in the middle density and higher as the density either increased or decreased. This might be interpreted in the light of discussions by Allee (*op. cit.*) as an illustration under field conditions of the undercrowding effect on mortality. This possible conclusion is clouded by the fact that the density of plot 1 was lower than the lowest in the pens, yet it had a lower apparent death rate instead of higher, as would be expected. The average rate of loss for all toads in plot 3 is greater, 15.14, compared with 10.03 for plot 1. The greater death rates in the experimental plot may be partially explained by (1) as noted in the description of plot 3, the fences acted as an exceptionally good collector of organisms and the predators might have concentrated their efforts here, and thus at the same time taken more toads, or (2) the fact that the density of plot 3 was double that of plot 1, gave another example of the direct density-dependent mortality relationship. At any rate, direct comparisons between toad-loss in plot 1 and plot 3 were not conclusive because of the fences that collected the toads and other animals. This may pro-

vide an unverified and experimentally unanalyzed example of relatively adverse effects on survival of both undercrowding and of overcrowding; however, conditions of this experiment make it difficult to draw such a conclusion since the data are not adequate for statistical examination.

SUMMARY

1. The activity of *Scaphiopus holbrooki* was studied statistically and the limits and variability of response to environmental factors were defined. It was shown that (a) toads emerged from their burrows in the order of 29 nights annually, while the number of known consecutive days underground averaged about ten days; burrow emergence was associated with certain temperatures, amounts of rainfall, relative humidities, seasons, and general weather types; (b) the rate of nocturnal activity varies with time of night, temperature, atmospheric humidity, amount of daily rainfall, and general weather type; (c) the emergence of toads from burrows was not at random with regard to time. Nights of activity for individuals tended to be concentrated in short periods of time with much longer times when no surface activity was apparent.

2. The food of spadefoots as illustrated by stomach contents was mostly comprised by beetles, Orthoptera, ants, lepidopterous larvae, and spiders living on the forest floor.

3. The distance toads moved from a known burrow to feed averaged 3.66 ft. and the modal class was two and less feet. The distance of feeding movements from a known burrow (a) was not different for males and females, (b) was greater for small toads than for larger ones, for toads in the ecotone than in the hammock, greater during spring and fall than during the winter months, greater during lower vapor pressure deficits than higher ones, (c) was greater during medium temperatures rather than extreme ones and (d) greater in populations of low density than under higher densities.

4. Spadefoot toads aggregate in certain major communities, especially in forests without considerable leaf detritus. There is a strong tendency towards aggregation within a non-homogeneous major habitat, the greater frequencies associated with sparse shrub vegetation. The distribution of burrows within an homogeneous habitat was a random and showed no aggregational trends. Records of capture sites in uniform hammock illustrated the same relationship, but in the ecotone there was evidence that although the burrows were spatially at random, the capture sites had a contagious distribution.

5. The size of the home range averaged 108.4 sq. ft., extremes being from 7 to 892, and if only 90% of the captures, those nearest the center of the range, were plotted, the range averaged 67.7 sq. ft. Ranges were greater (the difference not being significant) for females, for toads living in the ecotone rather than in the hammock, and for toads studied a longer period of time. Range size was associated with the number of captures of individuals and with the number of burrows recorded within a particular toad's range.

6. Records of 89 shifts of burrow location averaged 10.8 ft. and the length of time used averaged 106 days. Thirty-one toads moved their burrows but never returned, while eight alternated their utilization of from 2 to 5 burrows.

7. The ranges of a majority of the toads were linear or rectilinear shaped. The ranges of members of the same sex did not overlap generally and avoidance behavior was interpreted in the relationships between several toads in movements of their home range. These data led to the conclusion that territoriality was exhibited. The micro-habitat influenced the direction of movement from the burrow. In a choice between movement into densely or sparsely vegetated areas the toads moved into the more open areas. Observations indicated that the toads were spatially well orientated within their home range area.

8. Homing behavior, over extended round-trip distances, was observed when 7 toads were caught in the home plot before breeding, at distances between the plot and breeding ponds as great as $\frac{1}{4}$ mile, and then back at their point of departure later. Three females with eggs were handled in the plot before breeding and then observed at the same site later with no ovarian eggs, which led to the conclusion that they had returned from a breeding pond. Trapping evidence during the August, 1953, reproduction also denoted the homing reaction.

9. The dispersal of the adult population (a) was shown by studying the influx of new toads into the plots to be directly connected with occurrence of rainfall with the greatest changes occurring during the four breeding seasons of this study; (b) was negligible during the summer 1953, except for the August reproductive migrations; (c) was examined by studying the greatest distances between capture points for the whole study, seasonal and monthly periods and found to be mostly of very short movements; the records of long distances generally covered a considerable length of time.

10. Density estimation (a) was very inaccurate using the method of simply counting the number observed, the reason being that the toads were not active enough on the ground surface to be observed in short field studies; (b) was accomplished by counting the toads seen in a census period and adding those handled before and after the period under consideration and it produced quite good results for plot 3; this estimate was low for periods near the end of the study; (c) was accomplished using a rectilinear and a curvilinear index method and the results were compared; the difference between the two methods was not great; (d) using the index methods was not too reliable since it was shown that the marked population did not mix equally with the total population as a result of the non-random activity-time relationship discussed above; the failure of the assumption that released toads mixed at random in the total population was related to the underestimation of the population by the use of these index methods; (e) using the curvilinear equation produced mark-and-release indices very close to one; this meant that the proba-

bility of observing marked toads equaled that of finding new animals. The indices less than one denoted greater probability of capture for marked animals, and were reported mostly during the summer periods where (1) less dispersal movements decreased the chance of new animals being introduced, (2) there were smaller numbers of active toads, thus increasing the chance of capture of marked animals and (3) the smaller active population increased the chance for toad locations and habits to be learned by the observer. The indices greater than one, where there was greater probability of capture for new animals, occurred when breeding movements increased dispersal.

11. The results of density analysis (a) indicated that the density of toads in the ecotone was about double that of the hammock habitat. The density of the natural situation was about half that of the semi-controlled population; (b) illustrated that the lowest beginning population density of plot 3 was in the same order of magnitude as that of plot 1, the former being 493 and the latter between 400-500 toads per ac.; (c) reflected the lack of effective reproductive success during the study, since density continuously decreased during the 26 months of study.

12. During the course of this study, four breeding choruses were recorded, on September 18, 1951, February 15, 1952, April 7, and August 23, 1953, in conjunction with heavy rains of stationary frontal weather. There was evidence that breeding was connected with large amounts of rainfall.

13. The production of young toads in the 1951 reproduction was very small, none at all for 1952, slight (i.e., 6.7% of total population) for April, 1953, and considerable for the August, 1953 period.

14. Head width was utilized for the study of body growth since it was a more reliable and consistent measurement than others taken. The relationship between head width and interorbital span and total body length was expressed by rectilinear equations. Concerning development and growth (a) the age from metamorphosis was known only for a few toads produced in September, 1951, while age was extrapolated for other data; (b) definite external sex characteristics were observed to distinguish males and females when, on the average, they were 15 and 19 months of age, respectively; (c) growth in body size continually declined as the individuals grew older and larger; (d) significant sexual divergence in rate of growth was illustrated with the males growing at a faster rate and attaining a larger size; (e) the level of density was shown to hold an inversely proportional relationship with the rate of growth; (f) field records of head width growth for 11 males and 11 females were presented; (g) a theoretical growth curve through 8 years of life was extrapolated to express statistically the average rate of increase.

15. Frequency distributions of head width were plotted for males, females, and juveniles to examine the age group distribution of the population throughout the study. The relative number of young de-

creased and the older group frequencies increased as a result of poor breeding success. In the first period, about half of the group was less than 2 years old, while in the summer of 1953, about 22% were that old. Likewise, the per cent of toads with age estimated greater than 6 years was about 15% at the beginning and 39% at the end of the study. The population showed signs of aging.

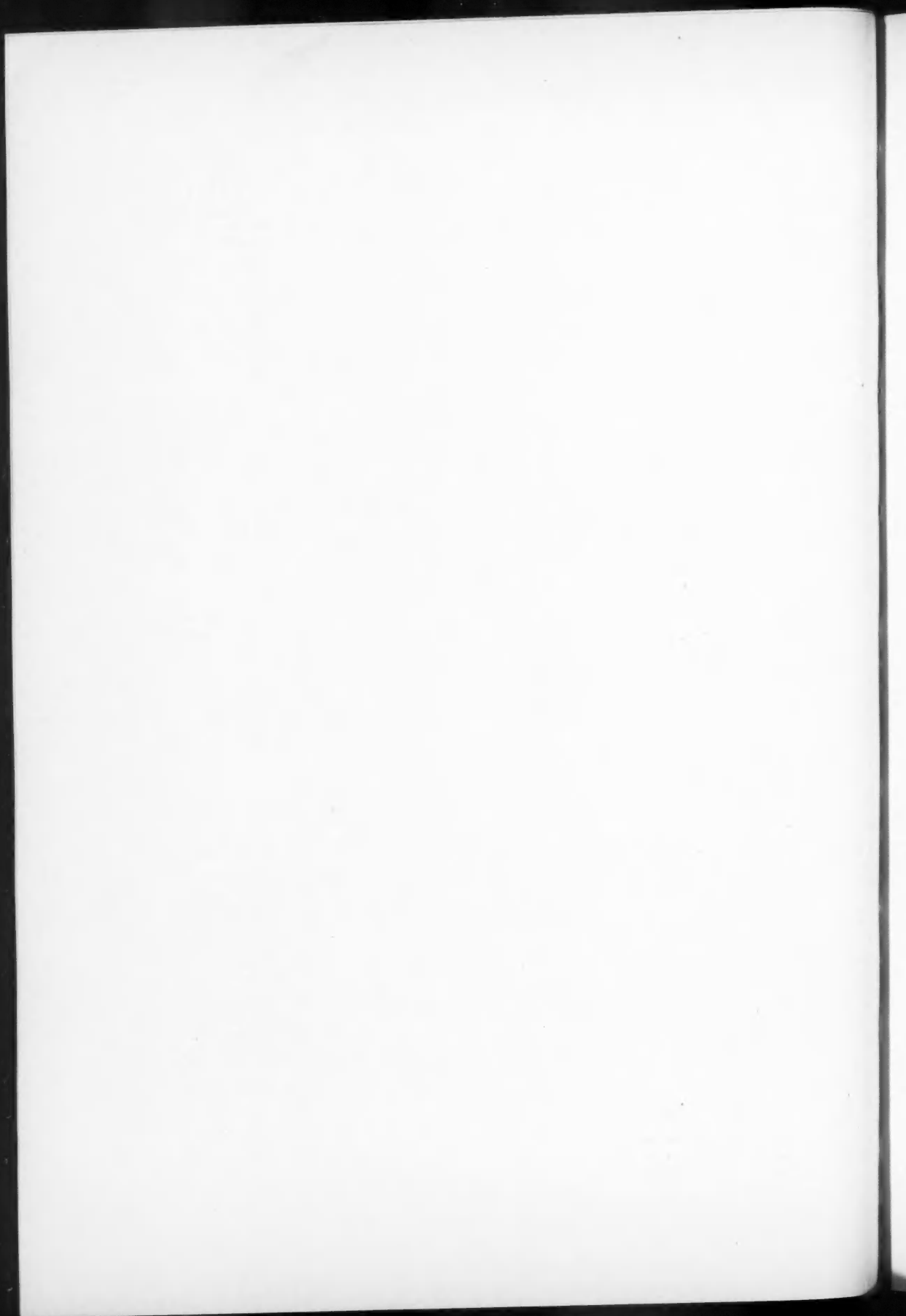
16. Disappearance rate was studied and concerning loss of toads (a) no evidence of predation on adults was secured in this study and published records are few; (b) the rate of loss seemed to be highest for toads beginning with head width 14 mm and less, lowest for toads 15-17 mm and high again for older toads with head width 18 mm and greater; (c) average rates of loss were lowest in middle densities, highest in the largest populations of the semi-controlled experimental group, and also nearly as high in the lowest density; it appeared that the middle density was optimum for survival with lower and higher density having lower values; the lowest density was about the same as that found in the natural field plot that had a low rate of loss; (d) there was no significant difference in rates of loss for males and females; (e) there was some evidence from plot 1 that disappearance rate was higher during breeding periods in 1951 and 1952; (f) there seemed to be a seasonal variation in losses with highest rates during June-August, and March-May, September-November, and December-February decreasing in that order; the winter periods of least activity rate exhibit the lowest losses and there may be a functional relationship between these observations; (g) the average departure rate for plot 1 was 10.0 toads per 100 per 3 months and 15.14 toads per 3 months in plot 3. The higher rates of disappearance in the experimental area was probably related to the aggregation of animals by the fences, thus making better grounds for predators. The density of the total experimental area was about double that of plot 1, so the increased rate of loss of the former could also be a result of the higher population size.

17. The percentage survival curve for *Scaphiopus* in this study from egg to old age can be roughly sketched. There was some evidence that survival percentage drops suddenly and sharply during egg, larval stages, and through burrow establishment. The rate of survival then decreases only slowly with young terrestrial individuals having a lower rate of survival than those, say, from 16-17 mm head width. As the toad reaches ages where the head width is 18 mm and greater, the survival values decrease again, possibly being associated with attainment of the physiological life span. This type of survival curve would possibly be described as a positive skew curve, as given by Allee, et al. (1949).

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STUDIES ON POPULATION PRODUCTIVITY

I. THREE APPROACHES TO THE OPTIMUM YIELD PROBLEM IN POPULATIONS OF *TRIBOLIUM CONFUSUM*

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TABLE OF CONTENTS

	PAGE		PAGE
INTRODUCTION	269	THIRD APPROACH: A MATHEMATICAL MODEL OF PRODUCTIVITY	279
MATERIALS AND METHODS	270	DISCUSSION	285
FIRST APPROACH: THE STATISTICAL ANALYSIS OF TEMPORAL TRENDS	271	SUMMARY	288
SECOND APPROACH: THE GRAPHICAL REGRESSION ANALYSIS OF THREE TYPES OF PRODUCTIVITY	277	LITERATURE CITED	289

INTRODUCTION

The optimum yield problem consists of determining the maximum number of individuals that can be removed from a population without impairing the ability of the remainder to produce this maximum over and over again. This problem arises whenever a population of living organisms is subjected to systematic exploitation by man, whether this be in the form of fishing, hunting, harvesting or lumbering. However, the fisheries' biologists have been largely responsible for the conceptual development of the problem.

The aim in this paper is not to solve specific practical problems arising from commercial fisheries or other systematically harvested resources, but rather to explore the theory of optimum yield from several points of view, in the conceptual framework of theoretical and laboratory population ecology.

Several features make the flour beetle, *Tribolium confusum*, excellent material with which to explore the theory of optimum yield in the laboratory. It is a small animal (about three mm long), large numbers may be raised, and several replicates of each harvesting procedure may be tested. It has a life cycle of about 30 days, so that effects of a given removal procedure may be followed for many generations. *Tribolium* lives in flour, so the whole population may be easily censused immediately prior to each removal. A great deal of previous work has been done on *Tribolium* which provides background information useful in husbandry, censusing, and the construction of a mathematical model. Also, it follows from the many years of work done on this species in the laboratories of Professor Thomas Park that the available stocks may be presumed to be inbred. All stages of *Tribolium* may be handled quickly without danger of destruction—a point not true of the young stages of many aquatic forms. Several age classes may be readily distinguished without the aid of optical instru-

ments or time-consuming examination and this, for example, would not be true of fish.

Three different types of analysis have been applied to the data obtained from this experiment: the statistical analysis of temporal population trends, graphical regression analysis, and analysis by means of a mathematical model. Each of these contributes a sort of information not readily available from the other two. The statistical analysis of population trends is most useful for determining the effects of given rates of exploitation. It shows if any treatment continued long enough will produce extinction, and gives insight into the mechanisms of oscillation and fluctuation, and the variability of results from a given rate of exploitation. The other two types of analysis are developed in terms of the number and age distribution of the individuals remaining after fishing, rather than the rate of exploitation. Graphical regression analysis, for phenomena involving a large number of independent variables, is the fastest, easiest way to obtain a detailed picture of the form of the function relating the dependent variable to the independent variables. A mathematical model may provide information about the dynamics of the system, and give results for which estimates of reliability can be obtained, a factor not true in the case of multi-dimensional graphs (Ezekiel 1941). A model also allows for an exact solution, provided it is a sufficiently realistic description of the system under exploitation.

Three terms will be defined in accordance with recent usage by Clarke, Macfadyen and Widrig. "Standing crop" will indicate the amount of beetles (expressed as either numbers or biomass) present at the time of census and prior to the removal of any individuals (following Clarke 1946). "Productivity" will signify the net amount of matter produced by a replicate in 30 days, and may refer to a number or biomass (Macfadyen 1948). The number or biomass removed at each census as a fraction of the standing

crop will be referred to as "the rate of exploitation" (Widrig 1954).

The theory of optimum yield conceived as a problem in population dynamics appears to have originated with Baranov (1918). He considered such problems as the relation of yield and fishing effort, and the effect of rate of exploitation on the age composition of the stock. The field received great impetus from a paper by Russell (1931), who outlined many of the factors involved in the problem. Subsequently, Hjort, Jahn & Ottestad (1933) related the optimum yield problem to the theory associated with the logistic curve. Some other papers which have made an important contribution to the evolution of thinking about this problem are those of Thompson & Bell (1934), Graham (1935), Thompson (1937), Sette (1943), Herrington (1944) and Nesbit (1944). Miller (1949) describes the effects of overfishing in a specific instance. Ricker (1944, 1945, 1954) has been influential in developing the modern mathematical approach to this problem. The most extensive recent mathematical developments are due to Beverton and his associates (Beverton, 1953). The literature in this field is very extensive, and a complete discussion will not be attempted here. Some of the above papers, and others, will be discussed later in regard to various aspects of the theory.

This paper results from work done under the direction of Professor Thomas Park, to whom I am indebted, for suggesting the problem, and for being patient and liberal with suggestions throughout the study. Many long and provocative conversations with Dr. Dennis Strawbridge have helped a great deal in crystallizing some of my ideas. Dr. J. Murray Speirs very kindly took time to check details in the entire manuscript in final form. Mr. Raymond Ammar, Dr. Bertram Hanna, Mr. Monte Lloyd, Dr. Herman Slatis and Mrs. Janice Spofford have read portions of the manuscript and offered numerous suggestions. These suggestions have been particularly helpful in the task of attempting to combine clarity and brevity within the framework of conventional mathematical notation in the section on the model. All statements in this paper, however, are the sole responsibility of the author.

MATERIALS AND METHODS

This investigation was started differently from the usual *Tribolium* populational experiment. Rather than beginning the experiment with a small number of adult beetles, an attempt was made to start the experiment with synthetic equilibrium age distributions. This was done in order to avoid waiting about a year for the populations to come to approximately equilibrium age composition. Complete information was not available on the age structure of a *Tribolium* population in equilibrium at the time this experiment was begun. Hence some arbitrary assumptions, now known to be incorrect, were made and each replicate was started with the age distribution shown in Table 1.

On the basis of information now available, including earlier work of Strawbridge (1953), we now know

that an equilibrium population contains a much higher percentage of old adults than was at first assumed. Park's equilibrium data for these physical conditions showed about 68% adults in the populations, instead of 62%, as here (Park 1954).

One hundred and eighty replicates were begun with the population composition as shown in Table 1. The universe for each replicate was 8 gms of medium in a 9.5 x 2.5 cm shell vial. The medium has been described by Park (1948). The medium was replaced each census, that is, every 30 days. The vials were kept in a dark incubator at 29.4°C ($\pm 0.07^\circ$) and 69% R.H. ($\pm 2.8\%$).

TABLE 1. Age composition of each replicate at initiation of experiment.

Age group	Males	Females	Totals
Small larvae.....	50
Large larvae.....	26
Pupae.....	6	6	12
Adults 0-29 days old.....	18	18	36
Adults 30-59 days old.....	15	15	30
Adults 60-89 days old.....	13	13	26
Adults 90-119 days old.....	9	9	18
Adults over 119 days old.....	15	15	30
Total.....	228

The 180 populations were censused at 30 days and 60 days without removal of any individuals. The census procedure was essentially the same as that described by Park (1948). Larvae were counted in two size categories. In every tenth population, the pupae were sexed with a binocular microscope. Neither high adult productivity nor high total numerical productivity caused a statistically significant change in the sex ratio. In every third population the standing crop, including eggs, was weighed on an analytical balance for the first 270 days of the experiment. Beginning with day 300, the standing crop, and remainder after "fishing," were weighed for each population. Eggs were counted at 300, 330, and 360 days for all populations. This gave a body of data with which to check the egg mortality equations in the mathematical model indicated later.

The study was started with a stock of washed eggs. Instruments, finger bowls, and bolting cloth were sterilized in an oven at 110°C. Three sets of each of the foregoing were rotated, the table top and counting dish were swabbed with alcohol between censuses, and in general elaborate precautions were taken to avoid contamination of the populations by the sporozoan *Adelina*. A description of the effect of this pathogen on *Tribolium* populations has been given by Park (1948).

Records were kept of all dead larvae seen through the course of the experiment. This was to determine what could be considered a normal background mortality, so that if a pathogen began to have a significant effect on any population, it would be immediately apparent. Normal background mortality turned

out to be about one larva in every 700 counted. This never showed an increase in any vial; it was a rare event to find two or more dead larvae in any vial. A typical pattern was to find a dead larva, then another at a census six or seven months later. Hence it seems reasonable to conclude that pathogens present were not populationally significant.

The experimental design appears in Table 2. Four different rates of exploitation were used in the initial design. Within each of these, there were three age distributions of the total removal. The exact procedure at each census may be made clear by an example. Let us consider a replicate in which the rate of exploitation is .3, and .25 is the fraction of the total removal consisting of adults. At each census, the larvae, in two size categories, pupae and adults were counted. The sum of these counts was multiplied by .3 to give the number of animals of all stages to be removed. This last number was then multiplied by .25 to give the number of adults in the total removal. The proportion of pupae in the remainder of the removal was then determined from the ratio of pupae to larvae in the standing crop.

TABLE 2. Experimental design.

INITIAL DESIGN (beginning day 90)			FINAL DESIGN (beginning day 300)		
Rate of Exploitation	Fraction of total removal consisting of adults	Replication	Rate of Exploitation	Fraction of total removal consisting of adults	Replication
.2.....	1.0	20	.2.....	1.0	5
.2.....	.75	12	.4.....	1.0	12
.2.....	.25	12	.5.....	1.0	12
.3.....	1.0	12	.4.....	.75	12
.3.....	.75	12	.5.....	.75	12
.3.....	.25	12	.2.....	.25	12
.4.....	1.0	12	.3.....	.25	12
.4.....	.75	12	.4.....	.25	12
.4.....	.25	12	.5.....	.25	11
.5.....	1.0	12	.6.....	.25	14
.5.....	.75	12	.7.....	.25	12
.5.....	.25	12	.8.....	.25	12
			.9.....	.25	12
Controls.....		20	Controls.....		20
Controls later used in pilot experiment....		8			
Totals.....		180	Totals.....		170

Removals according to the initial design were begun with the 90 day census, treatments being randomized with regard to the spacing of vials in the incubator.

The design was altered by changing the treatments of four of the replicate cohorts on the 300th day. This change was made because of information obtained from a pilot experiment that was run concurrently with the main experiment. The pilot experiment began on day 120. In eight of the controls all the adults and pupae and half the large larvae were removed at each census. These eight replicates showed that it was possible to obtain much higher productivi-

ties than were being obtained from even the highest rates of exploitation in the original design.

Hence at day 300, 14 of the replicates which had been subjected to a rate of exploitation of .2 with the adult removal 1.0 of the whole removal were shifted to a .6, .25 regimen. All the replicates in the .2, .75; .3, 1.0 and .3, .75 cohorts were shifted to treatments of .7, .25; .8, .25 and .9, .25 respectively.

The standing crop totals in this experiment exclude eggs. The only temporal trend data which include eggs are the measures of biomass productivity. Almost all the results discussed hereafter were obtained by analysis of productivity data. Three indices of productivity will be used: total numerical productivity, total biomass productivity, and adult numerical productivity. Productivity, the net amount of material, expressed either as numbers or biomass, produced by a replicate in 30 days, is obtained by subtracting the amount of material remaining after removal at time t from the standing crop at time $t + 30$ days. For example, in replicate no. 117, 233 mg of material was left behind after removal at day 300. The standing crop at day 330 was 287 mg. Hence the biomass productivity in the 30 days following day 300 was $287 - 233 = 54$ mg. It should be noted that any of the three productivity indices can be negative, indicating a decrease in this category. Also, adult numerical productivity can exceed total numerical productivity. An example will illustrate how this can occur. Suppose the remainder at time t consisted of 169 individuals, of which 10 were adults. Then if the standing crop at time $t + 30$ days was 297, including 156 adults, the total numerical productivity in the interval would have been $297 - 169 = 128$, and the adult numerical productivity would have been $156 - 10 = 146$.

FIRST APPROACH. THE STATISTICAL ANALYSIS OF TEMPORAL TRENDS

The aim of this approach was to analyze the results obtained when the data were averaged for each cohort of replicates subjected to a given rate, and age distribution of exploitation. This was different from the analyses used in the second and third approaches. For the last cases, treatment was ignored, and the data for each time for each replicate were classified according to the number and age distribution of the individuals left in the vials.

The statistical analysis of temporal trends consisted of an exploration of the effects of two independent variables, rate and age distribution of exploitation, on four dependent variables, the standing crop, total numerical productivity, total biomass productivity, and adult numerical productivity. The dependent variables were measured for each replicate and averaged for each treatment. Four different types of effects were considered for each dependent variable: temporal population trends; mean levels averaged for all times; fluctuations and oscillations of cohort means, and variability within cohorts. The plan of

the following discussion is to consider each of the four classes of effects in turn.

No removal regimen in Table 2 caused extinction of a single replicate. However all of the eight replicates in the pilot experiment were decimated by the treatment of removing all the adults and pupae and half the large larvae at each census. The analysis of decline is well documented by four replicates selected for this purpose and described in Table 3. The rates of exploitation given in this table are obtained by dividing the sum of the individuals removed (i.e. the adults, pupae and half the large larvae) by the total standing crop. For example, in replicate no. 29, at day 150, 192 adults, 86 pupae and 11 large larvae were removed. Hence the rate of exploitation was $199/249 = .80$.

TABLE 3. Analysis of decimation in four pilot experiment replicates.

Replicate number	Variable	AGE OF REPLICATES IN DAYS				
		120	150	180	210	240
29	Standing crop.....	289	249	242	124	81
	Rate of exploitation.....	.65	.80	.67	.98	..
	Small larvae remaining.....	59	38	81	3	..
	Large larvae remaining.....	41	11	0	0	..
	Adult numerical productivity.....	102	123	114	67	..
	Total numerical productivity.....	149	193	43	78	..
44	Standing crop.....	355	290	244	99	21
	Rate of exploitation.....	.63	.76	.86	1.00	..
	Small larvae remaining.....	82	60	35	0	..
	Large larvae remaining.....	51	10	0	0	..
	Adult numerical productivity.....	126	171	82	15	..
	Total numerical productivity.....	157	174	64	24	..
152	Standing crop.....	346	354	260	333	93
	Rate of exploitation.....	.65	.74	.50	.81	..
	Small larvae remaining.....	56	45	125	64	..
	Large larvae remaining.....	65	47	3	1	..
	Adult numerical productivity.....	153	101	245	82	..
	Total numerical productivity.....	233	168	205	28	..
177	Standing crop.....	345	305	221	227	49
	Rate of exploitation.....	.56	.84	.33	.99	..
	Small larvae remaining.....	115	38	148	3	..
	Large larvae remaining.....	37	11	0	0	..
	Adult numerical productivity.....	166	61	213	47	..
	Total numerical productivity.....	153	172	79	46	..

Some interesting points are made by the data in this table. The largest decreases in total numerical productivity are brought about in all four cases by rates of exploitation of less than 90%. In replicate no. 29 removal of only 67% of the standing crop at day 180 reduced the total numerical productivity from 193 to 43. In replicate no. 177 there is a very striking case at day 180. Here, a rate of exploitation of only .33 had a very serious effect on the population productivity. Evidently under certain conditions, repeated removal of under 70% of the standing crop could prevent the population from reconstituting itself and could thereby lead to decimation. However, it will be shown in a later section

that the optimum yield regimen is one in which at least 83% of the standing crop is removed at each harvest. The reason for this apparent anomaly is the different age distribution of the populations remaining in the two cases. The optimum yield regimen is one in which a small number of adults are left behind. The regimens in the pilot experiment led to decimation because in these cases only small larvae were left behind, and in some cases a few large larvae. This demonstrates the need for any optimum yield regimen to take into account the age distribution, as well as the size of the harvest which may be removed from a population without destroying the ability of the remainder to replace the removed individuals.

The data in Table 3 suggests that where the productivity does exceed zero, and where only a small number of small larvae were left behind (e.g. day 210, replicate 177), the productivity is due to hatching of eggs remaining at the beginning of the interval. The productivity is too small in such cases to necessitate the postulate that during the 30 days, small larvae reached adulthood and layed eggs which hatched. Hence, when all the fecund stock is removed together with the animals which will become fecund well before the end of the interval, the tremendous decrease in mortality owing to intraspecific competition does not compensate for the elimination of fecund individuals. This would not necessarily be true, say, for certain fish species in which the intraspecific competition at the fry stage might be even greater than it is in the flour beetle, and the fecundity is very high. In such cases, the best possible yield procedure might be one in which fecund individuals were only allowed to accumulate every second year.

A third point of interest that emerges from Table 3 concerns the ratio of the total numerical productivity to the adult numerical productivity. One of the characteristics of a decimated population is that almost all of the productivity consists of adults. In other words, eggs remaining at time t , where the population left behind is small, have a very good chance of becoming adults by time $t + 30$ days. This produces the higher adult productivity seen at $t + 30$. However, almost no eggs are laid after time t , because most of the fecund segment of the population has been removed. Hence there will be few pre-imagoes at time $t + 30$. Since under the yield regimen used in the pilot experiment, only half the large larvae, the small larvae and the eggs were allowed to remain, there will be few fecund individuals left in the interval $t + 30$ to $t + 60$ days. Hence removal according to the pilot experiment regimen will cause collapse of the population at time $t + 60$ in this situation. One of the danger signals that a population is being over-exploited can evidently be a shifting age distribution of the produced individuals.

Figure 1 illustrates the effect of different rates of exploitation on standing crop level. It will shortly become apparent that the standing crop level is useless as an index of productivity, or of the ability of the population to support a greatly increased pro-

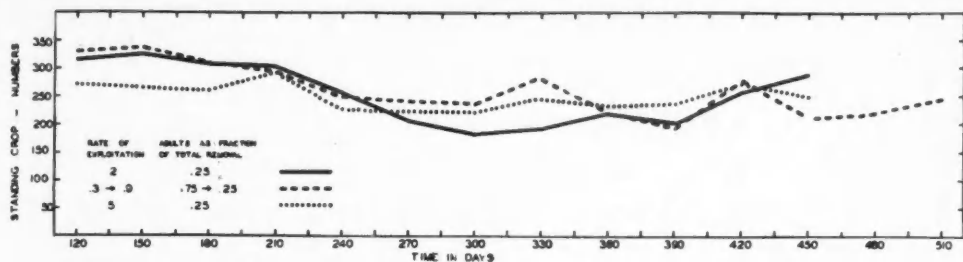


FIG. 1. Temporal trends of standing crop numbers for different rates of exploitation. The arrow indicates that the treatment was changed at day 300.

ductivity. The only standing crop level of the three illustrated which ever showed a steady downward trend was that for the lowest rate of exploitation, .2. Since this declined steadily from day 150 to day 300, it could be argued that a drop in standing crop level may not mean that a population is being decimated, but rather that it is not being exploited enough. It seems likely that the mechanism causing this decline in standing crop, in such a lightly-harvested cohort, was accumulation of old adults. Strawbridge (1953) has presented data from which it may be seen that old adults accumulate, and diminish productivity through a combination of depressed fecundity and high cannibalism.

All productivity levels, unlike standing crop levels, are simple functions of the rate of exploitation. This is demonstrated in Figs. 2A, 2B, and 2C for the three classes of productivity, in each case averaged for all times. In all three cases, the rate of increase of productivity changes at least slightly as the optimum yield rate of exploitation is approached. If the intensities of exploitation had been further increased, it would be seen that these curves do not flatten out at an asymptote, then crash, but crash suddenly when a critical exploitation rate is reached. This point is documented by Figs. 7 and 9 in terms of the numbers and age distributions of the remaining individuals. The reason that the crash does not appear in Figs. 2A, 2B, and 2C is that at high rates of exploitation, there is great variability amongst the replicates being averaged, as will be brought out in discussion of Table 4. The fact that analysis in terms of treatment can conceal or mask such a crash is a strong argument in favor of analysis in terms of what is left behind. A comparison of Figs. 2A and 7 illustrates this point very clearly.

The question arises as to whether rate of exploitation affects total numerical productivity and total biomass productivity the same way. This is answered by Fig. 3. Evidently, the upper limit of biomass productivity is reached at a lower rate of exploitation, and the biomass productivity begins to flatten at a lower rate of exploitation than the numerical productivity. The explanation for this is that at high rates of exploitation the productivity of light small larvae is elevated due to increased fecundity with correspondingly low mortality of density dependent coaction origin. One other indication of a shift in the

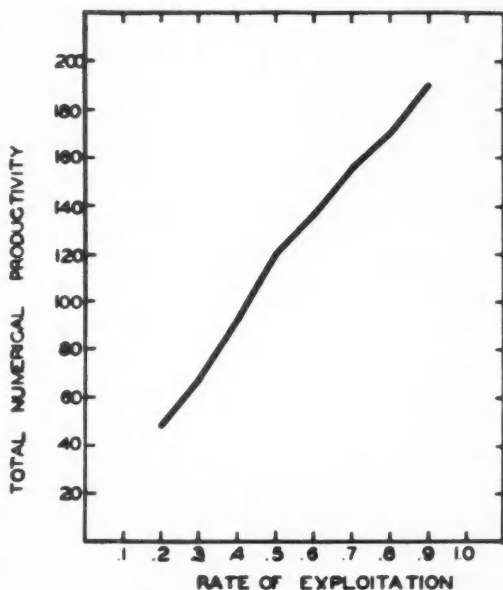


FIG. 2A. Total numerical productivity as a function of rate of exploitation.

age distribution of individuals produced with increased rate of exploitation is shown in Table 5 in which the total numerical productivity increases from 69 to 190, while the adult numerical productivity only rises from 24 to 41 for the same elevation in rate of exploitation.

The above suggests the generalization that the pattern of results from the same treatment may be different for different indices of productivity. This may be documented further by considering the effect of age distribution of exploitation on adult numerical productivity as compared to total numerical productivity. In Figure 4, the adult productivities for three different age distributions of exploitation and a rate of exploitation of .5 are plotted. The total numerical productivity for the same treatment is plotted in Fig. 5. There is a very striking difference in the adult productivity levels in Fig. 4, and just as striking a lack of difference in the total numerical productivity levels in Figure 5.

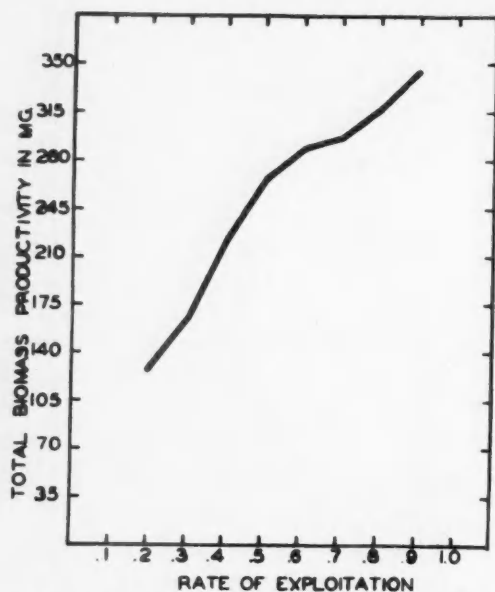


FIG. 2B. Total biomass productivity in mg. as a function of rate of exploitation.

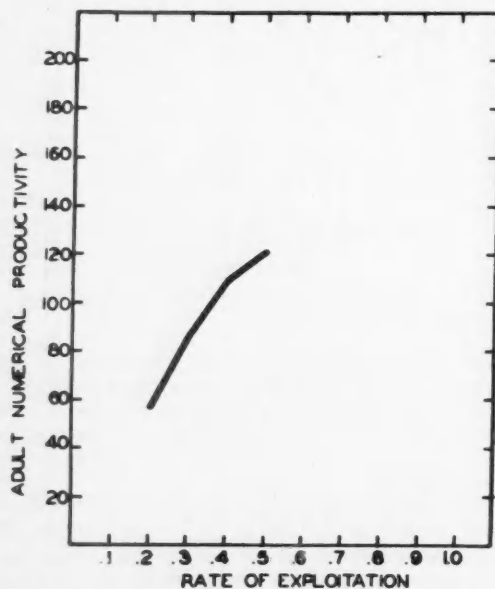


FIG. 2C. Adult numerical productivity as a function of rate of exploitation.

It has now been shown that all three classes of productivity are differently affected by any given treatment. The conclusion to be drawn from this is that any program designed to produce the maximum yield from a resource should involve a precise definition of the object of harvest.

Another point of considerable interest is documented by Figs. 4 and 5. The more adults that were

TABLE 4. Amplitude of oscillations and fluctuations, as a function of rate of exploitation.

Rate of exploitation*	VERTICAL DISTANCE FROM ZENITH TO NADIR DURING FINAL SEVEN-MONTH INTERVAL			
	Standing crop	Total numerical productivity	Total biomass productivity	Total adult productivity
.2	104.8	97.0	143.3†	23.2
.3	90.9	89.0	148.7	36.5
.4	101.6	94.5	158.3†	27.7
.5	51.3	30.7	96.0†	23.8
.6	77.4	77.9	143.7	67.7
.7	47.5	47.0	95.4	61.3
.8	47.3	49.3	118.2	50.1
.9	88.8	105.9	280.9	65.4

*In all cases the fraction of the total removal consisting of adults was .25.

†In the case of this treatment, only five months of data were available, so we can only say that the fluctuations in seven months would be equal to or greater than this.

TABLE 5. Variability and exploitation intensity for the last seven months of the experiment.

Dependent variable	Statistic	RATE OF EXPLOITATION*				
		.3	.6	.7	.8	.9
Standing crop	Mean	231.5	236.9	222.9	232.4	235.0
	Variance	2,641	2,855	2,930	†4,740	5,576
Total numerical productivity	Mean	69.2	135.5	155.8	171.2	189.8
	Variance	2,648	3,218	2,902	†5,969	6,861
Adult numerical productivity	Mean	23.8	33.2	37.1	38.3	40.8
	Variance	795	†1,469	1,491	2,084	2,066
Total biomass productivity	Mean	166.8	286.6	296.8	315.6	344.7
	Variance	8,659	†18,795	†12,295	†29,049	34,614

*In all cases .25 of the total removal consisted of adults.

†Indicates significant difference. The significance was tested using the 95 per cent fractiles in the table of variance ratios in Hald (1952).

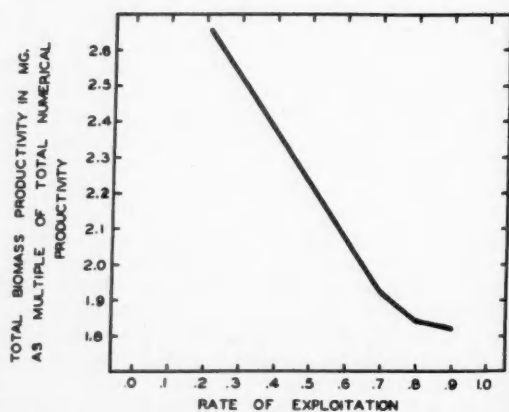


FIG. 3. Total biomass productivity in mg. as a multiple of total numerical productivity, as a function of rate of exploitation. The multiples for each rate of exploitation were obtained by averaging the data for the entire period the given rate of exploitation was continued.

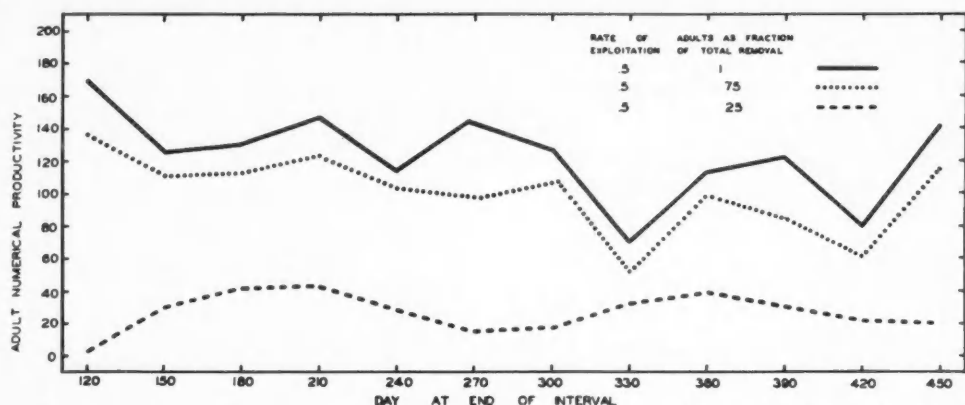


FIG. 4. Temporal trends of adult numerical productivities for three different age distributions of exploitation and a rate of exploitation of .5.

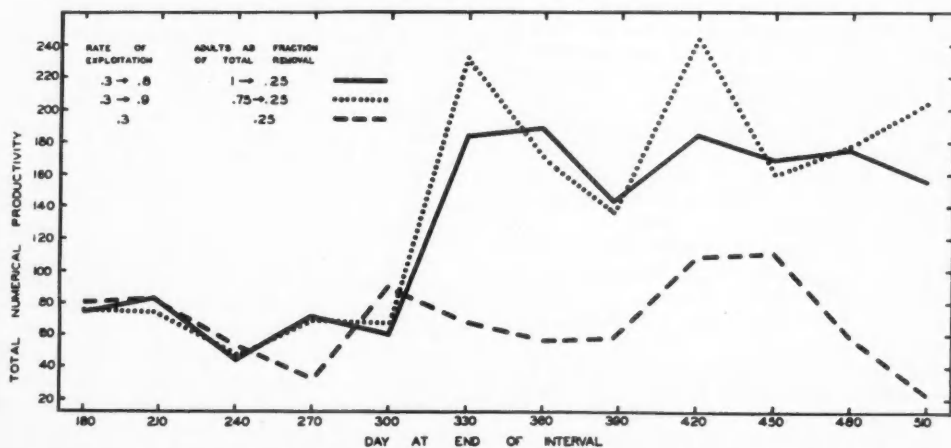
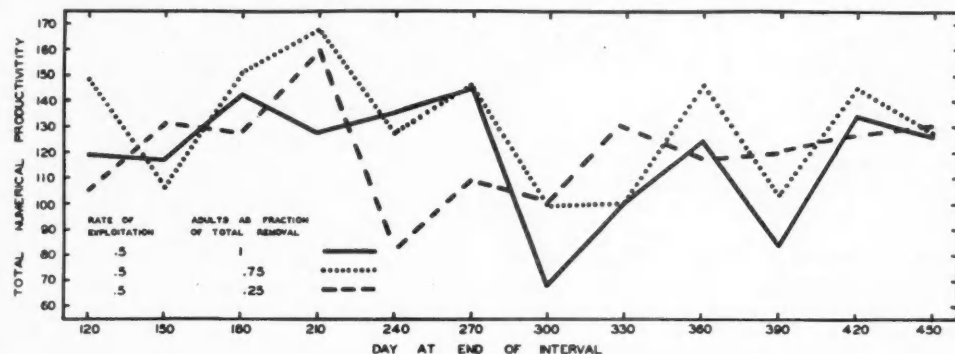


FIG. 5. Temporal trends of total numerical productivities for three different age distributions of exploitation and a rate of exploitation of .5.

FIG. 6. Temporal trends of total numerical productivities for three different rates of exploitation and the same age distribution of exploitation. The arrow indicates that the treatment was changed at day 300.

removed, the more were produced. But in all cases, the rate of exploitation of total numbers was the same, and the total numerical productivity was the same. Hence what is produced is related to what was

removed, and the populations tend to be homeostatic.

Some data on the relation of amplitude of fluctuations and oscillations to treatment are presented in Table 4. No relationships can be postulated with any

assurance because of the limited data. In order to make such statements the experiments would have to be continued for several years, and a much larger number of replicates would be necessary. However, certain possibilities are suggested by the data. In the table the last seven months have been considered in the case of each treatment to minimize the effect of another variable: damping of oscillations and fluctuations with time. The data given have been obtained by subtracting the lowest level reached by the cohort mean during the last seven months from the highest level reached. This was done for the standing crop temporal trends and the temporal trends for each of the three classes of productivity.

In the case of standing crop, total numerical productivity and total biomass productivity, the vertical distance from the nadir to the zenith during the final seven month period was great for the highest and lowest rates of exploitation, and least for some intermediate rate of exploitation. The rates for which the vertical distance was a minimum were in all cases close to the rates which produce optimum yield. These comments do not hold for the adult numerical productivity, but in this case the age distribution of the removal was very different from that which produces optimum yield of the yield category in question. Taking all these facts into consideration, the following is suggested as a tenable hypothesis. Fluctuations in level of standing crop and all classes of productivity are least when the rate and age distribution of exploitation are those which lead to optimum yield. Other exploitation regimens lead to greater amplitude in oscillations and fluctuations, and the more dissimilar the procedure from that which leads to optimum yield, the greater the fluctuation.

One possible cause of oscillation in under-exploited replicates is accumulation of old adults which lower the population fecundity and increase the mortality (Leslie & Park 1949; Strawbridge 1953; Rich 1954). The dynamics will be explored quantitatively in the section on the model. From the evidence available to date it appears that the positive phase of oscillation is produced by the accumulation of adults, and after a lag during which they pass over the peak of their age-fecundity curve the decline phase is caused by decreased fecundity and increased mortality.

Marked fluctuations occur after the rate of exploitation has surpassed the optimum yield exploitation rate. This suggests that these fluctuations are correlated with impairment of the ability of the populations to replace what is being removed. The marked fluctuations characteristic of overexploitation are exemplified by the upper line in Fig. 6. It is highly significant that the line just below it, for 8/9 as high a rate of exploitation, is much flatter.

There is some indication that oscillations and fluctuations of both standing crops and productivities become damped with time. However, the experiment would have to be run for several years to study this aspect of the problem adequately.

The tremendous productivity surges that follow big

increases in the rate of exploitation, such as those at day 330 in Fig. 6, underscore the magnitude of the intraspecific competition pressure in the vials. It is possible to remove 90% of the standing crop, then find an increased standing crop at the next harvest. This shows that over 90% of the original standing crop would have been destroyed in the interval by cannibalism or some other form of mortality of intraspecific coaction origin, or would not have been born at all due to depressed fecundity.

The information on the variability about the cohort mean for the last seven months of the experiment for five different treatments is presented in Table 5. The means have been given in each case to show that the increase in variability is not a simple function of the mean. For example, in the case of the standing crops, the variability for a rate of exploitation of .8 is significantly greater than the variability for .6, even though the mean is less.

One point is demonstrated very clearly by this table. Within each category there is a significant increase in the variability of the result with increase in the rate of exploitation. The best interpretation is possibly as follows. At high rates of exploitation there is a high probability that all the adults will be removed. In such cases there is a quite different situation with regard to intraspecific competition pressures than there is when at least a few adults remain (see the second and third approaches). The difference is increased if few or no pupae are left. Hence there is magnification of a difference by a threshold, and the variability of a cohort is increased if it contains a mixture of replicates above and below the threshold. Such threshold effects are important in lessening the reliability of mathematical models of productivity based on rate of exploitation, and provide us with the motive for focussing our attention on the segment of the population remaining in the vial after harvest, in the third approach.

Magnification of a difference by a threshold accounts for the anomalous situation pictured in the top line of Fig. 6. It is known from the analysis in the second approach that optimum yield occurs at about 90% removal (e.g. after day 300), but in this figure the 90% removal line has the marked fluctuations we would expect under overexploitation. Evidently some of the replicates in the cohort were over-exploited, while others were under-exploited. Even though the percentage removal is the same within a treatment, the age distribution of the remainders may be very different. Fig. 6 therefore provides another argument that analysis in terms of rate of exploitation, in contradistinction to the number and age distribution of remaining individuals, may be very misleading.

It would obviously be fallacious to attempt a complete analysis of the optimum yield problem in terms of rate of exploitation alone. Analysis in terms of treatment allows the lumping of dissimilar population age distributions and can mask what is occurring.

This is the reason for using the second and third approaches.

Before passing to the second approach, a summary of the major conclusions emerging from the analysis of standing crop and productivity temporal trends may be in order. Age distribution, as well as rate, of exploitation determines the consequences of a yield procedure. Standing crop levels indicate nothing about productivity. Productivity increases with rate of exploitation, up to a critical level. Different indices of productivity are differently affected by the same harvest technique, and therefore a scientific management program should include a precise definition of the object of harvest. Another point is that the populations tend to replace whatever age class is removed, and are therefore homeostatic. Population fluctuations are least at about optimum yield rate and age distribution of exploitation, and variability of standing crop and all classes of productivity increases with rate of exploitation, thereby casting doubt on the predictive reliability of models involving rate of exploitation.

SECOND APPROACH. THE GRAPHICAL REGRESSION ANALYSIS OF THREE TYPES OF PRODUCTIVITY

The aim of this approach was to determine graphically the form of the functional dependence of the three types of productivity on four independent variables. The four independent variables were the numbers of small larvae, large larvae, pupae and adults left in a vial after removal of the crop. The results of the analysis took the form of three large families of graphs, each of which was a pictorial representation of a five-dimensional hypersurface.

The technique of performing a graphic regression analysis of this type, wherein the net effect of the independent variables is joint rather than additive, has been described by Ezekiel (1941). Unfortunately, it is impossible to obtain estimates of reliability with a multi-dimensional graphic analysis (Ezekiel 1941) and this is one reason for using the third approach.

A single datum in this analysis consisted of the values of the four independent variables at census time t for one replicate, together with the values of the three dependent variables (i.e. the three indices of productivity) over the interval t to $t + 30$ days. In this analysis 2,266 such items were utilized. These were sorted into a $10 \times 6 \times 6 \times 4$, or 1440 cell matrix, according to variate-value ranges of adults, pupae, large and small larvae. This may seem like a large number of cells for such a small amount of data, but the data were aggregated in a certain part of the matrix. Only 499 of the 1440 cells contained any elements at all, 17 cells contained 20 or more entries, and one cell contained 245. Hence this sort of analysis can only reveal the character of the three hypersurfaces within rather limited boundaries, since extrapolation in five dimensions would be bound to be unreliable using a graphical technique.

In the case of adult productivity the inflexion point

has not been enclosed by the boundaries of the graphically determined hypersurface.

Figs. 7 and 9 are samples of the graphs obtained from the regression analysis of total numerical productivity. The maximum point on the line in Fig. 7 is the highest point in the productivity hypersurface showing up on any of the graphs obtained in the regression analysis. This need not be the highest productivity obtainable from a vial for the following reasons. First, the graphs may not even enclose the inflexion point. Second, we have only graphed selected plane projections of the hypersurface. The optimum yield point would only appear on the graphs if it happened to lie exactly on one of these planes. Herein is another argument for using the third approach. Once an equation for a hypersurface has been obtained, the inflexion point or points may be obtained immediately through calculus.

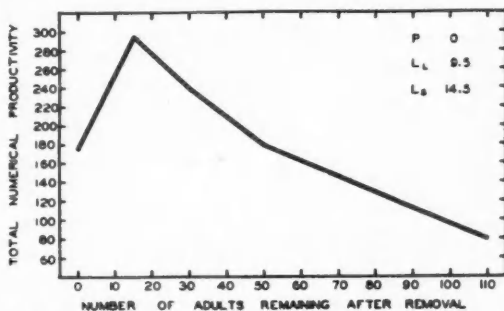


FIG. 7. Total numerical productivity as a function of the number of adults remaining after removal, when average values of pupae, large larvae and small larvae are held constant at 0, 9.5 and 14.5, respectively.

Six hundred graphs were drawn representing plane projections of various aspects of the three hypersurfaces using the technique of Ezekiel. A detailed verbal description of the shape of these hypersurfaces would be of little interest except perhaps to the specialist in research on *Tribolium*. However, several conclusions of more general interest emerge from an inspection of the shape of these hypersurfaces.

First, it is clear from a study of the productivity hypersurfaces that the net effect of the four independent variables is indeed joint rather than additive. An example of interaction of independent variables is shown in Fig. 9. However, much more complex examples than this could be demonstrated using sets selected from the 600 graphs drawn. The point is made, therefore, that the independent variables interact with each other so that the net result is not the sum of the results of the four independent variables. Hence this regression analysis has yielded population evidence for mortality of complex origin.

Second, the character of the hypersurface illustrates the sort of productivity collapse that follows overfishing. Fig. 7 demonstrates the collapse that results when the exploitation intensity is increased beyond the optimum yield point. This follows because a graph of productivity against remainder is equivalent

to a graph of productivity as a function of exploitation intensity plotted backwards. The noteworthy point here is that the productivity curve does not ascend, flatten out, then crash with increased numbers of adults removed. Rather, it ascends to a zenith, then plummets without warning. Hence the fact that productivity keeps rising with increasing rates of exploitation is in itself no guarantee that the exploiting agency is free from danger of decimating the resource if the rate of exploitation is increased slightly more.

The final point documented by the hypersurface for the total numerical productivity is that the age distribution of both the standing crop and the yield must be known before any rational management policy can be developed. For example, it is clear just from Fig. 9 without a knowledge of any other graphs, that if we were trying to maximize the productivity of a vial of beetles harvested every 30 days, it would make a great deal of difference whether the removal consisted of all but 105 small larvae and 15 adults, or 105 adults and 15 small larvae. In the former case the productivity would be 120 individuals, and in the latter 60, for this combination of pupae and large larvae left behind. The fact that the peak is at 15 adults and 15 small larvae remaining is an artifact that arises from grouping of data. In the regression analysis, all items with between 0 and 29 small larvae remaining were lumped. It is known from the pilot experiment that small larvae probably cannot contribute to the population fecundity in 30 days. All the new individuals recruited in 30 days when only small larvae remained can be explained by hatching of eggs present at the beginning of the interval.

While these populations have a total numerical strength under equilibrium conditions of about 230 individuals, they are able to reconstitute themselves from a reproducing stock of 39 individuals or less (Fig. 9). Hence in a yield procedure that allows 30 days for reconstitution, the populations can withstand a rate of exploitation that removes each census 83% or more of the standing crop. However, even though these populations have a tremendous reproductive potential, there exists a rate of exploitation that will decimate them.

The regression analysis of total biomass productivity revealed essentially the same general pattern of results as that for total numerical productivity. There were differences in detail, but this matter has already been illustrated by Fig. 3 and the adjoining discussion.

By far the most striking observations that arose from the regression analysis of adult numerical productivity were the following. First, it was much easier to obtain smooth curves from these data than from either of the other two kinds of productivity. This suggests that adult numerical productivity is a stochastic process involving less variability than the other two, and in which there are probably less component stochastic processes involved. Probably the pattern of the mesh of interacting factors is also less complex. Second, the pattern of the hypersurface in

this case is very different from that of either of the other two types of productivity. This is illustrated by a comparison of Figs. 8 and 9. These two figures each represent the planes of inspection for 10 pupae and 9.5 large larvae remaining. The three corresponding lines for small larvae are shown in each graph. (The other three have been omitted in each case for the sake of clarity.) Comparison of these figures shows how important it is that any optimum yield policy include a decision as to exactly what is the preferred object of harvest.

The variability of the stochastic process producing the preferred object of harvest is of importance in determining the reliability of a yield forecast. For example, if we were primarily interested in obtaining a maximum biomass productivity of all stages, it would not be possible to predict the outcome of a given harvest procedure with as much certainty as if we were interested in maximizing the productivity of numbers of adults.

The question arises as to what sort of population mechanisms have been evolved for the protection of the population in times of stress. Observation of cultures in very heavily conditioned medium shows that after a period of poor nutrition about all that remains of a population is a small number of adults. This is just the population composition that would produce a maximum total population. A very different population structure, with large numbers of larvae, would produce a maximum number of adults. But large numbers of larvae are definitely not found in cultures with heavily conditioned medium. It is conceivable that selection has been operating at the population level for a population structure producing the most advantageous age distribution with the return of favorable conditions. If this is so, what has been selected is a structure that will produce maximum total numbers, not a maximum number of adults.

The curves in Fig. 8 constitute another example of the tendency to homeostasis in these populations. The age compositions that make for maximum productivity of adults are those in which no adults are

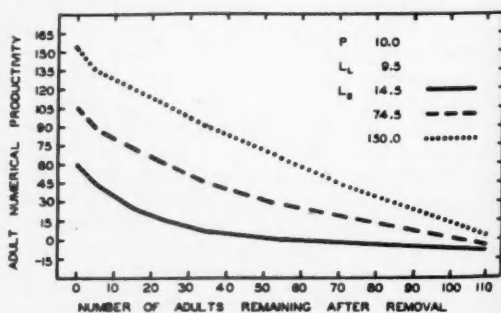


FIG. 8. Adult numerical productivity as a function of the number of adults remaining after removal, when the average values of pupae and large larvae remaining are held constant at 10.0 and 9.5. Three of the six lines for the average numbers of small larvae remaining are illustrated in order to demonstrate the effect of small larvae.

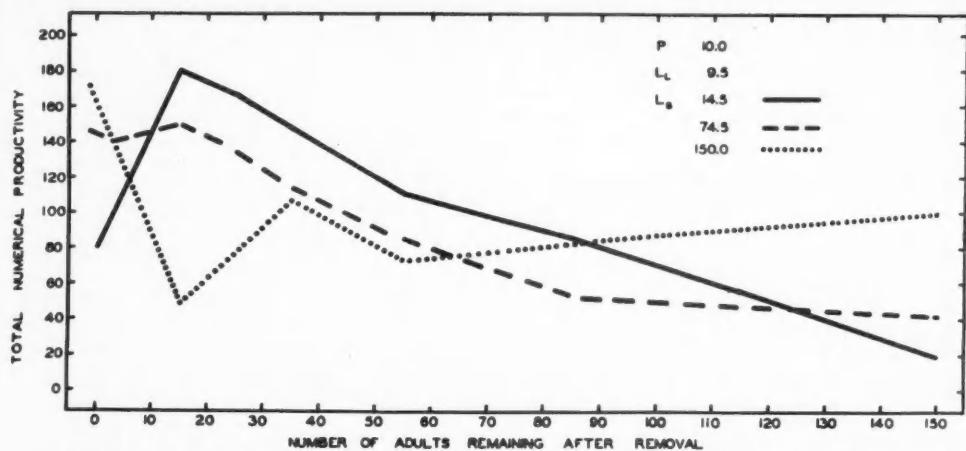


Fig. 9. Total numerical productivity as a function of the numbers of adults remaining after removal, when the average numbers of pupae and large larvae remaining in the vials are held constant at 10.0 and 9.5, respectively. Three of the six lines for the average numbers of small larvae remaining have been given in order to illustrate the joint rather than additive net effect of small larvae and adults.

present. This demonstrates again that what is produced is related to what was removed.

It is of interest to review the major conclusions from the graphical regression analysis, and assess the addition to the results already obtained from the temporal population trend analysis. The graphical analysis has confirmed two prior findings. First, the relation of age distribution of remainder after harvest to productivity must be known in order to solve the optimum yield problem. Second, the same treatment affects different indices of productivity differently. However, the graphical regression analysis has contributed two major points not obtained through the temporal population trend analysis. First, as rates of exploitation increase, productivity rises, then crashes at a critical level without first flattening off. Second, the form of interaction of the independent variables is joint, not additive.

THIRD APPROACH. A MATHEMATICAL MODEL OF PRODUCTIVITY

Two advantages of a mathematical model over a graphical regression analysis have already been mentioned. It is possible to get estimates of forecast reliability with a model but not with a set of graphs when there are over two independent variable. Also, calculus may be used on an equation to give a fast, completely objective technique of finding inflexion points and the values of the independent variables at which these points occur. In addition, an equation that is a real description of the system, in contradistinction to an algebraically fitted polynomial, can teach us a great deal about the dynamics of the system subjected to exploitation.

Any comprehensive theory of optimum yield must be flexible enough to handle two problems. The first is that of maximizing population fecundity, and the second is that of most efficiently exploiting the growth

potential of the stock already recruited. Important papers by Ricker (1954) on the first phase, and Ricker (1945) and Beverton (1953) on the second have added greatly to thinking about these matters. It would appear that a somewhat different approach would be useful if it could handle both of these problems simultaneously. That is, it would not only tell how to crop an age class in order to maximize its productivity, but also, how to maximize the size of the age class in the first place. Also, it should be sufficiently flexible to allow for various restrictions which may have to be placed on harvesting technique for practical reasons, varying open season lengths, and selection of a specific age class or classes as the preferred object of harvest.

Let us proceed by focusing our attention on the fraction of the population remaining after harvest, rather than the rate of exploitation. We must do this, because in the first approach it was shown that the predictive reliability of models based on the rate of exploitation would decrease sharply at high (i.e. optimum yield) rates due to failure to distinguish dissimilar age distributions of remainders. Also, this writer is convinced that to be completely realistic, a model for the determination of optimum yield procedure must take into account the different types of competition pressure exerted by the various age groups upon each other. The extent of the quantitative and qualitative differences between the effects of different age classes will be illustrated in the mathematical analysis of the beetle populations in this section. A very generalized treatment of three productivity models of increasing complexity is now given, considering the remainder subdivided into age classes.

CASE A. Maximum numerical productivity of all age classes is desired; no restrictions placed on harvest procedure.

Suppose that after harvest we leave behind n age

classes. Then we may say that the total productivity, numerical or biomass, when we fish the next time will be some joint curvilinear function of the number of individuals left behind in each of the n age classes. The curvilinear shape is due to pairs of antagonistic forces operating in the coactions that must be accounted for by the productivity function. For example, one sort of coaction that causes cannibalism to increase with density and another sort of coaction (e.g. interference) that causes cannibalism to decrease with density might interact to produce a roughly parabolic curve. The joint curvilinear function should include terms for every type of coaction that will affect the total yield. Where total numerical productivity is given by P_s , and the numbers in the various age classes left behind after harvest are given by x_a, x_b, \dots, x_n , we may write

$$P_s = F_s(x_a, x_b, \dots, x_n) \quad (1)$$

This is an equation for an n -dimensional hypersurface. The values of sets of the a to n x 's and the corresponding P 's are obtained empirically, and from large numbers of such sets, the form of F_s may be obtained through regression analysis. Or, better, the form of F_s may be obtained by deriving a model deductively, making use of a great deal of inductively obtained quantitative data, as has been done in the present instance.

The form in which (1) is written indicates that we are presupposing absolutely nothing about the form of interaction of the various independent variables with each other or with the dependent variable. The problem of optimum yield is that of finding a simultaneous solution for the values of x_a, x_b, \dots, x_n that maximize the value P_s during the interval from one harvest to the next. This is a standard problem in analysis. We get

$$\frac{\partial P_s}{\partial x_a} = \frac{\partial F_s(x_a, x_b, \dots, x_n)}{\partial x_a} \quad (2)$$

The same thing is done for each of the n independent variables. The n equations of similar form to (2) are then all equated to zero and solved simultaneously. The values for the n x 's thus obtained are those sizes of the n age classes which must be left behind after harvest in order to get a maximum numerical productivity in the interval prior to the next harvest. In this case, as in cases B and C, the procedure for obtaining a function and solution for biomass productivity is the same as that for numerical productivity.

CASE B. Specific age class is preferred object of harvest; no restrictions imposed on technique of harvest.

Generally, for technical or commercial reasons, only a certain age constituent of the total population is selected for harvest. For example, fish less than one year of age are rarely harvested. Very old fish use up an increasingly high fraction of their total energy input as energy output rather than growth, and consequently have a rate of growth curve that flattens out with increasing age (Allen 1951; Jobes 1952). The same thing is true for many other types of har-

vested organisms. Some organisms have an age-fecundity curve which rises to a peak, then falls (Leslie & Park 1949), although this may not be true in any fish populations (Allen 1951; Fry 1949).

Suppose age class i is the preferred object of harvest (although i could apply equally well to a group of age classes). In this case the productivity of i may be written as

$$P_i = F_i(x_a, x_b, \dots, x_n) \quad (3)$$

After obtaining the form of this function, the procedure is the same as in case A.

CASE C. Specific age class is preferred object of harvest; restrictions imposed on technique of harvest.

This is the most common type of case in commercially harvested populations, and is the type illustrated by this study. Suppose that for some technical or economic reason it is infeasible to remove or manipulate the numbers in some of the age classes of the exploited population. For example, in the present laboratory situation, no attempt was made to manipulate the numbers of eggs remaining after removal. In the commercial situations, it is generally infeasible to remove eggs or spawn, and addition of spawn has a negligible effect except in certain cases (Rounsefell & Everhart 1953).

Hence there are limitations to the extent that we can manipulate competition for the purpose of maximizing yield. In cases with restrictions and for this type of model, while there are n age classes and hence n intraspecific population variables that may be considered as density-dependent factors governing productivity, only k of these, say, are liable to manipulation. Hence we will only have k equations in the set corresponding to set (2), and $n-k$ of the variables will have to be treated as constants, the particular values for any harvest time being those actually found in the population. Otherwise the procedure is the same as in case A.

These are three very simple examples of the application of this type of approach. In each case, only intraspecific coaction factors were accounted for by the array of independent variables. However, such independent variables as interspecific competition pressure, predation, parasitism, abundance of food, and summed day-degrees of heat experience over a critical period in the life history could be included in the right hand side of the equation. Also, the approach can be extended to handle alternating closed and open seasons of varying lengths, fluctuating environment, and a preferred object of harvest which is a complex of species and age classes.

Solution of the optimum yield problem therefore reduces to the procedure of getting an equation in the form of equation (3). There are three techniques by which such an equation could be obtained to fit the data from the present experiment. Three criteria were used for deciding which of the three techniques to employ. Statistical proof that the model actually fitted the data had to:

1. vindicate the form of the model

2. vindicate the theory from which the model was derived
3. vindicate the usefulness of the model as a tool for objective interpolation.

Any method of deriving the equation for the productivity hypersurface which contained veiled circular reasoning would not meet these criteria. That is, it would yield an equation which was forced to fit the data to which it was applied. Hence proof that it did in fact fit would not constitute vindication of any of the above three points. The three techniques, evaluated according to these criteria, are discussed in the following paragraphs.

The model could be constructed by doing a regression analysis of the data. In this case both the mathematical structure of the model and the numerical values of the constants would be dictated by the data being analyzed. However, it is known from prior empirical studies of *Tribolium* population coactions in the laboratories of Professor Park that the model must handle eight elementary processes at least, and all the complex coactions arising from interplay of these. If the system is this complex, then obviously it will take a complex mathematical structure with a few dozen parameters to describe it. But it is clear that the form of the model becomes of diminishing significance in a regression analysis as the number of constants increases. With several dozen constants it would be quite possible to obtain a satisfactory fit to a host of different mathematical structures. Hence no matter how good the observed fit is to the data using this approach, it is impossible to prove that the model has any biological meaning. Therefore, this approach does not vindicate points (1) and (2). Also, the model would be merely an interpolatory procedure, and forcing it to fit n points would provide a very weak guarantee that it would fit an $n + 1$ th. point in the case of such a complex polynomial. It would be useless for prediction, and would not meet the third criterion.

A second possibility would be to get the form of the model deductively, using outside information or pure reasoning, then obtain the numerical values of the constants through regression analysis. However, this would not eliminate any of the above objections, since the large number of constants would make any given equation almost infinitely flexible, particularly in the case of a six-dimensional hypersurface. The model would again be merely an interpolatory procedure.

A third possible method would be to obtain, entirely from sources outside the data, both the mathematical structure of the model and the empirical data needed for the constants. This technique has been used in the construction of the model used in this study. If such a model gave results in good agreement with the data observed in this experiment, this would be highly significant. It would vindicate the form of the model, the theory from which it was derived, and the usefulness of the model as a tool for objective interpolation. In this case, no degrees of

freedom are lost by using data from the experiment in construction of the model to be tested against the data, and a mediocre fit is the best we have any right to expect. Hence a very good fit would constitute a powerful vindication, no matter how complex the model is. This is of prime importance in the present instance wherein the model gains further interest if it provides an actual description of the population mechanism.

Information for this model has come from several sources: the data on developmental time constants from Park & Frank (1948) and information about adult longevity from Pearl, Park & Miner (1941). Much information about survival of the various age classes under populational conditions was required. The form of presentation had to be such that the data could be analyzed and equations derived from them. Considerable knowledge of two species of *Tribolium* is available. However only data that were "analytical" as opposed to "populational" (Park 1954) and that were technically applicable to our experimental results could be used. To illustrate what is meant by this last statement, the data from Rich's (1954) analytical experiment were almost perfectly collected, yet too perfectly for use in this model. He did not consider an egg as alive unless it was plump and seemed to have an excellent chance of being fertile. Hence when few cannibals were present, there was very slight egg mortality in his experiment.

On the other hand, Strawbridge (1953) counted all eggs, as was done in the present experiment, and he reported eggs had a 37% mortality when few cannibals were present. The egg mortality equations revealed by regression analysis of the data of these two workers were naturally quite different. Strawbridge (1953) presents data from a populational experiment which seem to have been collected in a manner nearly identical to that of the present study, with the exception of his use of three, rather than two larval categories. The advisability of converting this segment of the data from one species to another, and treating developmental time constants as density-independent, and the technique of making all the necessary conversions will be discussed later.

The following conventions are used throughout the development of the model with regard to symbols.

- A Adult beetles over six days of age.
- Y Young adult beetles from time of casting of pupal skin to end of sixth day of adult age.
- P Pupae.
- L Large larvae.
- S Small larvae.
- E Eggs.
- P_A Net productivity of adults, i.e. the number of adults found at any census less the number of adults left behind 30 days previously. This number may be negative.

Subscripts refer to times. For example, A_{30} refers to the number of adults at 30 days. Superscripts refer to the age class present at the previous census

which has given rise to the stage under consideration. For example, A^P refers to adults that have been formed from pupae present at the last census. Hence P_{18}^S refers to pupae which were formed from small larvae present at the beginning of the 30 day interval. The pupae are at the 18 day mark of the 30 day interval, on an average for the age cohort.

The objective is to obtain an equation for P_A in the form of (3) and then treat this as outlined for the set of equations (2). We want $P_A = A_{30} - A_0$, which can be evaluated from

$$P_A = (A_{30}^A + A_{30}^P + A_{30}^L + A_{30}^S + A_{30}^E) - A_0 \quad (4)$$

From a numerical standpoint, the aim is to get a model from which numerical coefficients of two-figure accuracy can be obtained. Only two-figure accuracy is needed because the multiplicands corresponding to the coefficients are generally only two-digit numbers. In general, the coefficients are sufficiently small two-digit numbers that an error of four per cent in the calculation of the coefficient will only result in an error of one in the second significant figure of the coefficient itself.

Certain assumptions and simplifications have been used in the development of this model. The results seem to justify their use as will shortly be made evident.

Park (1938) and Park, Miller & Lutherman (1939) have shown that developmental time constants are density-dependent. However, analysis of the data from this experiment and that of Strawbridge reveals no need to postulate varying time constants. The explanation for this apparent anomaly appears to be as follows. In the range of densities which lengthen the time for development, cannibalism is so great that an individual either develops in the times given by Park & Frank (1948) or else gets a negligible chance of moulting to the next stage. According to Strawbridge's data, cannibalism is as high as 14% per day for large larvae, and 20% per day for pupae and young adults. Hence, even though the developmental time constants are density-dependent, for the purpose of deriving this model they may be treated as if they were density-independent. It is assumed that the error introduced this way is negligible.

The model will be developed on deterministic, rather than stochastic assumptions, and all the animals of any age will be treated as if they moulted at exactly the same time. In reality the times of moulting could be expressed only as a probability function. Also, it shall be assumed that if the time elapsed in any stage is x days, all the animals found in that stage at time of census are exactly $x/2$ days through the stage. In reality, this would be the mean age, and a probability function would be needed for the age distribution at time 0 days.

Another assumption underlies the use of Strawbridge's data on *Tribolium castaneum* (1953) for this model dealing with *T. confusum*, namely: that from a populational standpoint, at 29°C and 70% R.H., the chief differences between the two species are fecundity,

developmental time constants, and adult longevity. We assume that the other intraspecies coactions are sufficiently similar quantitatively and qualitatively so that equations from one species will yield values for the mortality coefficients of the other having a reliability within four per cent.

Other assumptions will be pointed out at the time they are introduced.

At certain points in the development of this model, two or more equations will have to be employed for the same relationship. For example, regression analysis of Strawbridge's data shows that under certain conditions cannibalism of young adults is given by

$$\frac{dY}{dt} = -Y(-.00827 + .0032A_0 - .0000157A_0^2) \quad (5)$$

It is clear that this equation could not possibly hold in the range $A \leq 2$, because if it did, multiplication by a coefficient derived from this equation would produce the ridiculous result of increase in the number of young. The explanation for this apparent incongruity, which occurs several times in the model, is that no cannibalism occurs at all unless a certain population density of cannibals is present.

The device for handling cases like this has been to use alternative sets of equations. In the above example (5), the relation holds in the range $A_0 \geq 3$, and the alternative equation for the range

$$A_0 \leq 2 \text{ is } \frac{dY}{dt} = 0.$$

A complete exposition of the development of this model would be extremely lengthy, hence three methods have been adopted to achieve brevity and, also, point up the essential principles on which the theory is constructed. In the first place, the discussion of the derivation of the numerical values of the constants will be kept very brief. Only the source of the data used will be indicated. Second, the numerical values of the constants will not be used in the presentation of the technique of derivation. All of these will be substituted into one of the alternative forms for the complete productivity hypersurface equation at the completion of the derivation. The values of the constants have been obtained by analysis of the graphs in Strawbridge's thesis. In most cases, the procedure was to read off a series of pairs of points, then fit an equation to the table of data so obtained by regression analysis. Third, none of the alternative forms will be introduced other than two: equations (12) and (13).

We shall now proceed to construct the equations for the terms in (4). Each of the terms of form A_{30}^x in (4) will be evaluated by obtaining, for the group that was of age x at time 0, the product of the probabilities of survival during each of its life stages up to time 30.

From Pearl, Park & Miner (1941), it is possible to obtain the data necessary to develop an equation for adult mortality. The data of the present experiment show that high productivity of adults only occurs

when there are less than 100 adults for eight grams of flour. However, we also know that this small number of adults is almost always an indication of high adult turnover rates, due to fairly intense harvesting. Under such conditions it seems reasonable to assume that an adult has essentially no chance of living beyond 120 days due to the combined effects of natural and fishing mortality. Accurate information about adult age-structure is not available, so we must be content with the un-weighted mean age. This will not constitute much of an error, since the adult mortality curves are relatively flat throughout the central part of the range 6 to 120 days, and mortality through most of this age span is very slight. From Table 3 (Pearl, Park & Miner 1941) we may take the form of the mortality equation to be

$$\frac{dA}{dt} = -aA, \text{ and integrating, we get}$$

$$A_{30} = A_0 e^{-30a} \quad (6)$$

for the number of adults surviving the 30 days.

The next step is to find the number of pupae at time 0 that survive to form adults 30 days later. Since all the survival equations have been developed in the same way, this one will be explained in some detail as an example and thereafter no explanations will be given. The first sub-step is to find the number of pupae hatching at an average time of 2.9 days. It is assumed throughout that x beetles in eight grams of flour have essentially equal conditioning effect to that of $x/2$ in four grams. This conversion is necessary because Strawbridge used four grams of flour per vial instead of eight as in the present experiment. The form of the equation for the appropriate line in Strawbridge's Fig. 14 is

$$\frac{dP}{dt} = -P \left(1 - \frac{1}{1 + bA_0} \right).$$

This form indicates that cannibalism of pupae by adults rises to an asymptote with increasing adult densities, then levels off. The biological interpretation to be placed on the levelling off is not clear.

Correcting for eight grams, or twice as many beetles, we assume that the equation will become

$$\frac{dP}{dt} = -P \left(1 - \frac{1}{1 + bA_0/2} \right)$$

This makes clear the assumption that x beetles in eight grams of flour do about as much cannibalizing as $x/2$ in four grams. Correcting for one day, instead of three (Strawbridge expressed the mortality in fraction per three days), we get the form

$$\frac{dP}{dt} = -P \left(1/3 - \frac{1/3}{1 + bA_0/2} \right),$$

and integrating to get the number of pupae surviving to day 2.9, we have

$$P_{2.9} = P_0 e^{-2.9 \left(1/3 - \frac{1/3}{1 + bA_0/2} \right)} \quad (7).$$

From now on it should be understood (a) that in each equation we correct for the conditioning of the

medium, the number of grams of flour and the number of days, and (b) that all coefficients of mortality are expressed as decimals, not percentages. Conditioning is expressible quantitatively as the product of the average number of beetles in the flour and the time they have been in it since the flour was last changed.

The form of the equation for the cannibalism of young adults by old adults was obtained from the appropriate line in Strawbridge's Fig. 15. This line appears as a parabola. A plausible interpretation of such lines is that two density-dependent processes, cannibalism and interference with cannibalism due to some phenomenon associated with crowding, are operating against each other. This may be made more intuitively obvious if the parabola is expressed in the form

$$\frac{dY}{dt} = -Y (c + dA_0 (f - gA_0)).$$

However, from now on all parabolas will be written in the form

$$\frac{dY}{dt} = -Y (c + d f A_0 - d g A_0^2).$$

Making the appropriate corrections, and integrating over six days, we find that the number of young adults surviving to 8.9 days of the original cohort of pupae left behind at day 0 is given by the form

$$Y_{8.9}^P = P_{2.9} e^{-6(c + d f A_0 - d g A_0^2)} \quad (8).$$

Similarly, using the same information as for equation (6), we get as the number of adults surviving from day 8.9 to day 30,

$$A_{30}^P = Y_{8.9}^P e^{-21.1a} \quad (9)$$

From equations (7), (8) and (9), we get

$$A_{30}^P = P_0 e^{-2.9 \left(1/3 - \frac{1/3}{1 + bA_0/2} \right) - 6(c + d f A_0 - d g A_0^2) - 21.1a} \quad (10)$$

The remaining equations for the terms in equation (4) have all been constructed in a similar fashion.

Four complicating factors make the equations for the small larvae and egg mortality coefficients very complex.

First, the individuals that were pupae at day 0 have had enough time to become adults, and to function as cannibals, by the time the small larvae left behind at time 0 have pupated. Terms for cannibalism by adults (recently pupae) must of course include corrections for the cannibalism to which they have been subjected.

Second, this is the first set of equations in which a mortality component due to within-stage interference has been introduced. This mortality is a function of the density of the small larvae at risk of death. The underlying mechanism is not clear at present, and we would not be justified in labelling it as cannibalism. Up to 20% of the small larvae left behind at time 0 may be destroyed in the 30 day interval by this mortality. Mortality of a stage dependent on the density of that stage, but also dependent, and in a different

functional form, on the density of other stages, is difficult to handle mathematically. Differential equations for such relationships integrate to give very complex expressions. Hence, integration was avoided in this particular case only, in order to keep the whole equation for the productivity hypersurface as simple as possible. Instead of integrating to get a term of form

$$e^{-[f(A_0) + f(P_0) + f(S_0)]},$$

we adopted the device of using a term of form

$$1 - f(S_0)$$

and placing the other terms in the exponent.

Third, the mortality of what Strawbridge called medium larvae has been accounted for by inclusion in the mortality equations for small larvae. This mortality was a joint function of the density of adults and the density of small larvae. The equation was constructed by combining the data in Strawbridge's Figs. 8 and 10A.

Fourth, in the case of small larvae and eggs, by the time they had reached their late pre-imaginal stages where there was heavy cannibalism by adults, there had been a significant mortality of the principle cannibals, namely: the adults left behind at time 0.

The final small larva mortality equation involves 33 parameters and is therefore too complex to be given here, but is included in the final equation (12).

Finally, the egg mortality coefficient must be computed. According to Park & Frank (1948), the average time for imago-formation by an egg is $5.3 + 16.5 + 5.8 = 27.6$ days (adding the developmental times for the other three preimaginal stages to that for eggs). There is a low chance of survival (as low as .67 per day according to Strawbridge), if the sum of adults and large larvae exceeds 30, and a low chance of survival combined with a low number of eggs laid for less than 30 adults. Hence it is clear that the eggs laid after day 30 can make essentially no contribution to the number of adults present at day 30.

However, there is a mean of 117.6 eggs left behind per eight grams of flour, averaging across treatments (data from the present experiment), and these will make a sizable contribution to the number of adults found at time $t + 30$ days if the number of adults and large larvae left behind at time t is small.

Strawbridge's Figure 7A gives a fairly good fit to the following form

$$E_{2.65}^E = E_0 [1 - (a + bL - cL^2) - (d + fA - gA^2) + (a + bL - cL^2) (d + fA - gA^2)] \quad (11)$$

The notion that competing mortality forces should operate this way follows from the addition formula of the calculus of probabilities and was first used in the literature of population ecology by Thompson & Bell (1934).

The coefficient for egg survival will be the same as that for small larval survival to the accuracy that concerns us. There are two modifications needed, however. The egg mortality coefficient will be the

product of the right hand terms of the equation for small larva survival and equation (11), and one parameter must be changed slightly since the individuals starting the 30 day period as eggs will spend less time during the interval as adults than those starting the interval as small larvae.

Enough information has now been obtained to construct an equation for adult productivity. This equation is built by using equations (6), (10) and (11), and the equations for large and small larvae which were not given. One of the many alternative forms of the final equation, which holds for the ranges of values $S_0 < 110$, $L_0 > 0$, and $A_0 \geq 40$, is as follows.

$$\begin{aligned} P_A &= A_{30}^A + A_{30}^P + A_{30}^L + A_{30}^S + A_{30}^E - A_0 \\ &= .94A_0 + P_0 e^{Z_1(A_0)} + L_0 e^{Z_2(A_0)} \\ &\quad + \{ [1 - Z_3(S_0)] S_0 + [1 - Z_3(E_0)] E_0 \\ &\quad [1 - Z_4(L_0) - Z_5(A_0) + Z_4(L_0)Z_5(A_0)] e^{-0.0056} \} \\ &\quad \{ e^{-1.89 - .0232A_0 + Z_6(A_0) + Z_7(A_0, P_0) +} \\ &\quad Z_8(A_0, P_0) + Z_9(A_0, P_0) \} - A_0 \end{aligned} \quad (12)$$

$$\text{Where } Z_1(A_0) = \frac{-.952 - .0192A_0 + .0000942A_0^2 + .957}{1 + .0075A_0}$$

$$Z_2(A_0) = \frac{-2.118 - .0219A_0 + .0000935A_0^2 + 1.91}{1 + .0075A_0}$$

$$Z_3(S_0) = \frac{.2}{1 + e^{3.2 - .0645S_0}}$$

$$Z_4(L_0) = .34 + .0100L_0 - .0000495L_0^2$$

$$Z_5(A_0) = .33 + .00746 - .0000360A_0^2$$

$$Z_6(A_0) = \frac{4.125}{20 + .05A_0}$$

$$Z_7(A_0, P_0) = \frac{1.91}{1 + .0073A_0 + .0075P_0 e^{Z_1(A_0)} + .034}$$

$$Z_8(A_0, P_0) = -.0219P_0 e^{Z_1(A_0) + .024}$$

$$Z_9(A_0, P_0) = .0000996 [P_0 e^{Z_1(A_0) + .024} + .96A_0]^2$$

Before proceeding to the solution of this equation to determine the optimum yield, a discussion of the reliability of the model is in order. The standard error of estimate for the portion of the model covered by the condition $A_0 = 0$ is 35.1. For the whole hypersurface in the range of A_0 values under 100, the standard error of estimate is 39.9, for 39 parameters. The index of multiple correlation for the hypersurface in the range of A_0 values under 100 is .81. The last statistic means that 66% of the variability in the dependent variable is in common with variability in the independent variables. It is relevant to introduce a brief discussion of the sources of the unaccounted-

for 34% of the variability. These appear to be three in number.

1. Variability inherent in the biological system. That is, a series of replicates started with the identical age composition will not reach the end of a month with the same adult productivity.

2. Failure of the model to provide a complete description of the biological system. Many of the component processes are not accounted for, and many of them are as yet incompletely understood.

3. Inaccuracy of the model. Many assumptions have been made, and many of the equations represent extrapolations beyond the range of values for which data have been collected.

The first of the three points may be illustrated in two ways. Table 6 demonstrates that while the standard error of estimate for an individual replicate is 39.9, much of this unreliability of prediction vanishes when the items with a similar starting age distribution are lumped.

TABLE 6. Comparison of observed and calculated values for adult numerical productivity for various initial age distributions, when data of similar distributions are lumped.

n*	OBSERVED VALUES				CALCULATED MORTALITY COEFFICIENTS					ADULT NUMERICAL PRODUCTIVITY	
	\bar{A}_0	\bar{F}_0	\bar{L}_0	\bar{S}_0	A	P	L	S	E†	Calculated	Observed
7....	0	0	5	486	.64	.37	51	47
9....	0	9	0	4496	.86	.63	.39	82	88
8....	0	13	71	10096	.86	.70	.12	157	155
9....	23	14	7	74	.94	.59	.55	.41	.12	55	60
70....	57	9	1	47	.94	.35	.25	.19	.05	15	15
20....	49	10	3	99	.94	.38	.29	.25	.06	34	39
14....	58	13	26	43	.94	.34	.24	.19	.03	19	21
15....	55	25	2	50	.94	.35	.25	.21	.05	24	27
10....	82	0	0	0	.9404	0	-4
18....	87	10	4	104	.94	.27	.16	.14	.02	16	14
35....	119	13	48	76	.94	.25	.12	.09	.01	10	12
10....	121	11	49	104	.94	.25	.12	.10	.01	12	14

*Sample size.

†In all cases the number of eggs remaining at day 0 was taken to be 118, because the number of eggs was only counted during part of the experiment. 118 was the average number of eggs found at a census when eggs were counted.

Another empirical finding which bears on the inherent biological variability of these replicates can be seen from analysis of the data. The experiment was started with 180 replicates with the same age distribution. Also, each replicate had the same sex ratio among the adults and pupae. Even with these precautions, and a uniform temperature throughout the incubator, there was a standard deviation of 7.53 for the adult numerical productivity for the first 180 replicates at the end of the 30 days.

It is a reasonable conclusion that much of the inability of this model to make a perfect prediction of the outcome for any replicate is due to the natural biological variability of the system.

The use of sets of partial differential equations to get the inflexion point for this model would be extremely tedious without recourse to special computing

apparatus. The process of solution has been greatly simplified by starting with the information given by the graphical regression analysis of adult numerical productivity about adults and pupae. This analysis showed that the optimum yield point for adult numerical productivity would occur when $A_0 = P_0 = 0$. However, the graphical analysis did not yield a solution for L_0 and S_0 . All we could tell from the families of graphs was that the inflexion point occurred for values of these two independent variables that were probably not on the graphs. In other words, optimum yield for adult numerical productivity under these physical conditions occurs for some population age distribution which was not left behind in the present experiment.

Hence the solution now employed illustrates the way a graphical and mathematical solution can complement each other, and, also, the use of the mathematical model as a tool for objective extrapolation.

From this model and when the conditions are imposed that $A_0 = P_0 = 0$, the equation for the hypersurface becomes as follows. In order to illustrate case C, in which restrictions are imposed on method of harvest, the condition is imposed that $E_0 = 118$.

$$P_A = -.0459L_0 + .68S_0 - .00295S_0^2 + .0000313S_0^3 + 59.790 + .004484L_0^2 \quad (13)$$

Taking the partial derivative with respect to L_0 , the solution $L_0 = 5.1$ is obtained. Taking the partial derivative with respect to S_0 yields imaginary roots. The reason for this may be investigated by substituting 5.1 for L_0 in (13) and obtaining sets of P_A values for increasing values of S_0 . This operation shows that for increasing values of S_0 , the values of P_A rise slowly at first, then at an increasing rate. This is biologically unrealistic. The interpretation that seems most reasonable is that for $E_0 = 118$, and $A_0 = P_0 = 0$, optimum yield occurs at $L_0 = 5.1$ and at some very high number of small larvae (probably 200 or more).

The reason that the equation as presently constituted does not yield real roots for S_0 when we take the partial derivative is to be found in the method of derivation. The technique often involved extrapolation from existing information. Where the biological system produced a change in a curve beyond the point at which extrapolation was begun, this would not be described in the final equation for the productivity hypersurface.

DISCUSSION

Four themes broader in perspective than the conclusions already mentioned will be considered here. These are: first, the logistic curve and optimum yield theory; second, exploitation and homeostasis; third, the design of experiments for biological maximization problems and fourth, the management of commercially harvested populations.

At various times the sigmoid or logistic curve of population growth has come under criticism for a variety of reasons. Examples of different types of criticism are the papers of Wright (1926), Feller (1940), Smith (1952) and Slobodkin (1954). Owing

to the prominence and controversial nature of this curve in ecological theory, and its application to the theory of optimum yield by Hjort, Jahn & Ottestad (1933) and Ketchum, Lillick & Redfield (1949), it is of interest to examine the results of the present investigation in relation to the theory associated with the curve.

Gause (1934) used the form of the differential equation

$$\frac{dN}{dt} = \frac{bN(K-N)}{K}$$

where N is the population size, b the intrinsic rate of natural increase, t is time, and K the maximum number of individuals a given physico-chemical environment will support.

It is a commonplace that

$$\frac{d\left(\frac{dN}{dt}\right)}{dN} = b - \frac{2bN}{K},$$

and if this approach to the problem of optimum yield is valid, the maximum rate of population productivity will occur when $N = K/2$. Hence the technique of obtaining optimum yield, according to this school of thought, is to continually crop the population so that $K/2$ individuals are left behind.

In this experiment, the maximum size attained by any of the control populations was 400 beetles, so we may take K to be roughly 400. In the regression analysis, when the population is at about $N = K/2$, no age distribution produces over 5.4 beetles a day, whereas at $N = K/10$, the population can produce up to ten beetles a day. Hence, in this case the prediction based on the sigmoid curve is incorrect since it predicts that the productivity will be a maximum at $N = K/2$, which is in error by a factor of five.

The cause of this unreliability of prediction is due to an assumption implicit in the logistic approach to the optimum yield problem. The theory assumes that the age composition of K/x individuals remaining after harvest is the same as that of K/x individuals under conditions of initial population growth. This assumption does not hold for *Tribolium* populations. There, the same number of adults is present in $K/10$ individuals of all ages after harvest as would be present in $K/2$ individuals under the usual conditions of population growth. Hence, under normal conditions of harvest, we would expect maximum productivity to occur at some level of N less than $K/2$.

There has been great interest in the theory of auto-regulating mechanisms in the last ten years. Examples of recent papers which considered the population in this light are those of Emerson (1954) and Hutchinson (1954).

An obvious homeostatic mechanism has been pointed out previously, when it was noted that the age structure of the group of individuals produced tended to be similar to the age structure of the group previously removed. However, of somewhat more interest are the implications of the fact that oscillations and fluctuations are minimal at intermediate fishing levels.

Evidently, rate of exploitation can modify the auto-regulatory mechanism of the population. Hutchinson (1954) pointed out the relationship between homeostasis and fluctuations. Fluctuations are due to lag effects of the forces which tend to produce equilibrium in a population. Strawbridge (1953) has shown the relation between accumulation of old adults and oscillations. This is due to increased cannibalism and lowered fecundity caused by high adult density and increased mean adult age. This combination greatly diminishes the chance of formation of young adults. Hence, when the accumulated stock of old adults dies off in a body, there is a sharp population decline until new adults can build up in numbers and restore the population fecundity. Ricker (1954) has presented a detailed exposition of the relationship of adult densities to oscillation.

It thus seems reasonable to expect that increasing the rate of exploitation up to the optimum yield rate should diminish oscillation amplitude. This is because harvesting repeatedly prevents the accumulation of old adults. Thus the effect of depression of fecundity and elevation of cannibalism is smoothed out from one harvest to the next.

On the other hand, if the rate of exploitation is increased over the optimum yield rate, the population can no longer reconstitute itself. There will be an increase in population fluctuation amplitude over that occurring at the optimum yield rate of exploitation. This occurs because there will be shifting effects of cannibalism and fecundity each census interval in a declining population, and therefore no equilibrium level can be maintained. Oscillation amplitude is accordingly at a minimum at the optimum yield rate of exploitation.

The present investigation constitutes an example of the solution of a type of problem which is very common in applied ecology, that is, a maximization problem. For example, it is desired to maximize the harvest of deer, fish, wheat, or trees for a given set of physico-chemical conditions, or it is desired to maximize the total predation and parasitism pressure against a destructive insect pest, or noxious weed. In such cases, it would appear that the conceptual form of the problem is that of a function in which the dependent variable is the quantity to be maximized. This is expressed as some function of the independent variables, which include the quantities we can manipulate to obtain maximization. Before analysis, deductive or inductive, it would appear that a logically rigorous approach to the problem demands that this relationship be written in the form

$$Y = F(a, b, c, d, \dots, z),$$

thereby begging no questions about the form of the dependence. However, it is possible for a long-range program of experimentation to explore the relevant group of independent variables one, two or three at a time. Such an approach seems to assume that by subsequently fitting the results together, it would be possible to construct a model for the phenomenon in-

cluding the operation of all the independent variables.

It would appear that this piecemeal approach begs the question as to the form of the functional dependence of the dependent variable on the independent variables. If it is assumed that a valid model can be obtained by fitting together the results of a series of experiments, then we are logically forced to admit the corollary assumption that the form of the relationship is additive. That is,

$$Y = f_a(a) + f_b(b) + \dots + f_z(z).$$

Unless there is some prior empirical reason, or deductive justification for making this assumption, we have no right to believe that the piecemeal approach will in fact yield a model that has other than a crude resemblance to the situation in nature.

It can be argued that one of the components in the piecemeal approach that deals with only one independent variable and its functional relationship to the dependent variable will account for, say, 25% of the total variability of the system in nature. This is true, but the pattern of the effect of this 25% may be quite different than the pattern when other independent variables are allowed to assume varying values.

It appears that this is one of the most important points that was demonstrated by the present model. It will be noted that many of the terms are complex. For example, the cannibalism of eggs by large larvae is not at all independent of the cannibalism of eggs by adults. The two mortality forces in effect compete with each other for the objects of their force. Also, the cannibalism of one form by a second may often be modified by the presence of a third, or fourth life stage which eats the second. A model for total numerical productivity would be even more complex.

The way to investigate such interrelations seems to be to study nature directly, or else some experimental situation that approaches nature as closely as possible in that all relevant independent variables are allowed to vary freely within the ranges of values which are of interest. Then a joint regression analysis can be performed on the resulting data. This analysis can take two alternative forms. We can concern ourselves solely with obtaining a solution, in which case a regression analysis, algebraic or graphical, will suffice. In either case these would be strictly interpolatory procedures and would be less reliable as the number of independent variables and the complexity of the system increased. On the other hand, an attempt could be made to analyze mechanisms as well, in which case, a descriptive model of the general type developed in this study would be necessary.

This experiment has shown that certain characteristics must be possessed by any realistic model of optimum yield. These characteristics are specified in the following paragraphs.

1. Such a model must involve a precise definition as to exactly what is the object of harvest. It has been demonstrated in this investigation, for example, that the regimen which makes for high adult productivity is not at all the same as the procedure making for high total numerical productivity. In addition, it

has been shown that not only must a decision be made as to the age class or classes to be harvested, but also it must be decided if the objective is to maximize biomass or numbers.

2. The model must involve a carefully considered decision as to what part of the population we should exploit. In the present case, there would be no point in removing any small larvae if the aim was to maximize productivity of adults. Miller (1949) describes an example in which too young fish were exploited and the fishery collapsed.

3. A realistic model must take into consideration the age structure of the population left behind, and by so doing, take into account that fecundity, mortality and all coaction effects are functions of age. The need for this has been demonstrated by the three approaches in the present investigation, and by numerous other experimental studies and compilations of data on natural populations.

4. The model must allow for joint, as contrasted to additive net effects of the independent variables on the dependent variable (productivity).

5. It must utilize the absolute numbers of the population left behind. Admittedly, this is difficult information to obtain, but what is biologically important to the future history of any population is not what is taken away from it but what remains. The same removal from two populations having different initial standing crops will have utterly different effects in the two cases.

6. The model must yield an optimum yield fishing or harvesting procedure that allows the exploited population to take maximum advantage of the lower levels in the food pyramid (Fry 1949).

It would be foolhardy to attempt any detailed application of the results of this experiment to the situation generally encountered in commercial fisheries. Such situations have non-uniform environments, both spatially and temporally, involve many species, migrations, and a host of problems in sampling. However, if it is assumed that certain basic attributes are common to all populations of Metazoa, such as intraspecific competition, and varying mortality and fecundity with age, then some of the present findings suggest phenomena that may occur in these situations, and logical possibilities as to the mechanisms underlying these.

There is no assurance of the reliability of the standing crop level as an index of either the turnover rate or of the ability of the population to maintain a greatly increased turnover rate. This experiment has shown that a declining crop may not mean that a resource is exhausted, but rather that it is not being exploited enough. The lack of significance of the standing crop level shown here confirms current opinion among fisheries biologists (Clarke 1946; Sette 1943; Hile, Lunker & Buettner 1953).

The fact that increasing fishing intensities produce increasing yields is in itself no guarantee that we are far from the point of optimum yield. The regression curves for total productivity, a function of the num-

ber of adults remaining after fishing, show that yield may rise steadily as more and more individuals of a critical age group are removed, then crash suddenly. The yield does not warn of an impending crash by flattening out prior to the crash. Since intraspecific competition is usually very intense, the first effect of a greatly increased fishing intensity will generally be a surge in yield, even though this fishing intensity can decimate the population.

Another way of describing the same phenomenon is to note that the effect of a catastrophic fishing intensity need not show up for some time after it is applied, the length of time increasing with the intensity of the competition that occurs under usual conditions in the population.

Burkenroad (1952) has criticized other authors for making such statements as, "... a major catastrophe was imminent because the catch per unit of effort was on the decline, even though total catches continued to increase." Our results seem to support the position of Burkenroad, namely: that increased difficulty of capture may not mean that the ability of the stock to replace itself has been destroyed. The writer believes, like Burkenroad, that in the case of most fisheries, particularly oceanic fisheries, we do not have any notion what fishing intensity would be desirable. The present experiment has demonstrated how simple production statistics could be misleading. For example, inspection of Fig. 6 shows that very low productivity may be caused by too low, rather than too high a rate of exploitation (in addition to the environmental factors, of course). The lowest line in the figure drops off sharply from day 450 on, yet the resource could obviously stand a much higher rate of exploitation. Very low exploitation may cause the catch per unit effort to decline by keeping the population fecundity at a low level, or by keeping the intraspecific competition at too high a level. In both cases, the mechanism of the effect was accumulation of old adults. This substantiates the point already made that it is just as important to consider the age distribution of the remaining stock as its size. It may be that it is typically more likely to err on the side of leaving too many fecund individuals in the stock rather than too few. Every commercial fisherman with whom the author has discussed the point has noted that surges in yield often follow periods when the stock has fallen to a very low level. Possibly higher sustained yields would result if the fecund stock was always kept at the low levels apparently associated with the surges just mentioned.

There has been a great deal of discussion and controversy, particularly in the last six years, on the causes of fluctuations in abundance of commercially harvested fish populations (Burkenroad 1948, 1951; Schuck 1949; Langlois 1948; and many more). A succinct review of the various positions is given by J. M. Thomson (1953), who notes that in recent years several authorities have attributed the major fluctuations in fish abundance to varying environmental factors rather than fishing mortality.

The writer is obviously in no position to make any assertions about the role played by fishing in the fluctuation of fish stocks, or even to assert that fishing plays any role at all, on the basis of this experiment. However, he is justified in noting the existence of certain logical possibilities. First, since the fished stocks fluctuated in a relatively uniform environment, and since the pattern of the fluctuations in the fished stocks was different from the pattern of the fluctuations in unfished stocks (control populations), fishing can certainly play some part in the pattern of fluctuations in a population. This has always been assumed to be true. However, it has also been shown that fishing intensities (either higher or lower than the optimum yield intensity) may increase the amplitude of these fluctuations. This has evidently not been universally recognized, since at one point in his paper Thomson (1953) makes the following statement, "It seems doubtful whether the mullet fishery is very intense. It would therefore seem likely that the fluctuations in catch observed may be due to 'natural' causes."

Finally, this experiment has suggested that it may be unwise to attempt precise analysis of the exploitation of fish stocks with mathematical models involving the notion of rate of exploitation. The same rate of exploitation can have utterly different biological results if it leaves behind different sizes or age distributions of the populations remaining after removal of the harvest. The greater the rate of exploitation, the less reliable are the predictions of a model based on rate of exploitation.

SUMMARY

The effects on productivity of various rates, and age distributions of exploitation were tested on populations of the flour beetle *Tribolium confusum* Duval. One hundred and eighty replicates were run for periods of up to 17 months in a dark incubator at 29°C and 70% R.H. Censusing, replacement of flour and removal of beetles took place every 30 days.

The results of the experiment were assessed in terms of three different indices of productivity: total biomass productivity, total numerical productivity, and adult numerical productivity. The results were analyzed using three approaches: statistical analysis of temporal population trends, graphical regression analysis, and a mathematical model constructed to describe the interactions occurring in the populations.

Standing crop levels do not indicate either the productivity or the ability of the population to maintain greatly increased productivity. Age distributions, and numbers, of individuals remaining after removal of the harvest are the important factors in determining the consequences of harvest. Productivity increases with rate of exploitation, then crashes without warning of the impending crash by first flattening off. However, the variability of standing crop and all classes of productivity increases significantly with increased rates of exploitation. This suggests a possible source of weakness in mathematical models of productivity based on rate of exploitation. For this

reason, the model presented focussed attention, instead, on the individuals remaining after harvest.

The three indices of productivity were differently affected by the same treatment. Therefore a scientific program to harvest a resource should be based on a decision about the age of the preferred object of harvest and also whether numbers or biomass is the quantity to be maximized.

The populations were homeostatic in that the individuals replaced tended to be the same age as the individuals removed.

Fluctuations and oscillations of standing crop and productivity were least at intermediate fishing rates, because under such conditions the oscillation mechanism (accumulation of old adults) was broken up.

The form of interaction of the independent variables was joint, not additive.

The model employed 39 parameters and was developed using information from other experiments, in order not to lose degrees of freedom in testing the model against the data from this experiment. The model accounted for all but 34% of the variability in the system, and most of this 34% was due to biological variability between replicates.

The results of this experiment were not those predicted by the logistic curve; the discrepancy was due to an incorrect assumption about age structure in the logistic approach to the optimum yield problem.

Ecological maximization problems should probably be solved by letting all variables vary at once if there is reason to think that their action is joint rather than additive.

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TROPHIC STRUCTURE AND PRODUCTIVITY OF A WINDWARD CORAL REEF COMMUNITY ON ENIWETOK ATOLL¹

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TABLE OF CONTENTS

	PAGE		PAGE
INTRODUCTION	291	Consumers Other Than Corals	305
The Problem of Relating Standing Crop and Production	291	Herbivores	306
Acknowledgments	292	Carnivores Other Than Corals	309
General Procedures	293	Decomposers	309
THE WINDWARD REEF COMMUNITY, ZONATION OF AN INTER-ISLAND REEF	293	Biomass Pyramids	310
Windward Buttress Zone	293	COMMUNITY METABOLISM	310
Coral-Algal Ridge	294	Flux of Larger Plankton	312
Encrusting Zone	294	Total Organic Matter	313
Zone of Smaller Heads	295	Production and Respiration by the Flow Method..	314
Zone of Larger Heads	295	Production Experiments in Submerged Bell Jars and Plastic Bags	314
Zone of Sand and Shingle	297	Phosphorus and Nitrogen	315
Current Velocities	297	Reef Deposition, Reef Erosion, pH Changes	316
TROPHIC STRUCTURE	297	Balance Sheet for the Reef Community	317
Plant and Animal Components in Live Coral; The Predominance of Plant Protozoa	297	Efficiency	318
Primary Producers	302	Relationship between Trophic Structure and Community Metabolism	318
Corals as Consumers	305	SUMMARY	318
		LITERATURE CITED	319

INTRODUCTION

The coral reef communities of the world are tremendously varied associations of plants and animals growing luxuriantly in tropical waters of impoverished plankton content. Under intense equatorial insolation the plants apparently grow rapidly and are eaten rapidly. Save for fluctuations the reef seems unchanged year after year, and reefs apparently persist, at least intermittently, for millions of years. With such long periods of time, adjustments in organismal components have produced a biota with a successful competitive adjustment in a relatively constant environment. The reef community is famous for its immense concentrations of life and its complexity.

Perhaps in the structure of organization of this relatively isolated system man can learn about optima for utilizing sunlight and raw materials, for mankind's great civilization is not in steady state and its relation with nature seems to fluctuate erratically and dangerously. What, then, is the relationship between organic productivity, energetic efficiency, and the standing crop structure of a coral reef community? How are steady state equilibria such as the reef ecosystem self adjusted?

Since nuclear explosion tests are being conducted in the vicinity of these inherently stable reef communities, a unique opportunity is provided for critical assays of the effects of radiations due to fission products on whole populations and entire ecological systems in the field. In the present paper some results are presented of a variety of measurements made on an Eniwetok Atoll reef which as yet has been little affected by nuclear explosions. These measurements represent both a multiple approach to the problem of obtaining practical assays of total function which will aid future comparisons between the normal and the irradiated reef ecosystems, and also a continuing effort by many to answer the questions posed in the preceding paragraph.

THE PROBLEM OF RELATING STANDING CROP AND PRODUCTION

In recent years rapid advances in technique and approach have permitted the measurement of the metabolism and productivity (rate of production) of aquatic communities and their components. Ingenious methods such as used by Sargent & Austin (1949, 1954) building on the work of Mayor (1924), Yonge (1940), and others, have permitted estimates of the productivity of coral reefs. Intense post-war interest in the tropical Pacific by geologist and biologist alike has led to new and detailed popu-

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lation and zonal study of reef fauna and flora such as by Ladd, *et al.* (1950), Tracey, *et al.* (1948), Emery, *et al.* (1954), Wells (1951), Doty & Morrison (1954), and Cloud (1952, 1954). It seems now time to determine the relationship between the standing crop, defined as the dry biomass of existing organisms per area, and productivity, defined as the rate of manufacture of dry biomass per area.

It has long been felt that the productivity of the various trophic levels of a community is very roughly proportional to the standing crop being maintained although the reason has not been entirely clear. Many have confused these entirely different properties of ecosystems. The distributions of standing crop may be represented graphically by trophic level so as to form block diagrams in the shape of pyramids. For a discussion of pyramids and production see Odum, E. P. (1953). In another communication by Odum & Pinkerton (1955) theoretical reasoning based on the second law of thermodynamics is presented to show that systems of many types when in open steady state tend to adjust to maximum output of energy consistent with available input energy and a corresponding low but optimum efficiency. If steady state systems tend to be similarly self adjusted regarding efficiency of energy utilization between trophic levels, then there is theoretical reason for expecting pyramids of biomass to be similar for components with similar metabolic rates. It is pertinent that somewhat similar pyramids have been found in Silver Springs, Florida, a rich constant-temperature aquatic commu-

nity in slightly pulsing steady state (Odum, H. T. 1953), and in successional terrestrial communities in the Savannah River Atomic Energy Commission area of South Carolina (Odum, E. P. 1954).

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We are also indebted to L. D. Tuthill, Department of Zoology and R. W. Hiatt, Director of the Marine Laboratory of the University of Hawaii for providing facilities for the work done in Hawaii.

Identifications of organisms were provided by F. M. Bayer (corals), M. Doty (algae), C. E. Cuttress (anemones), R. Hiatt (invertebrates), and A. Weylander (fish). Code numbers have been assigned to unidentified corals along with tentative names to specimens deposited with the U. S. National Museum.



FIG. 1. Aerial view (July 1954) of the Japtan reef looking northeastward into the trade winds. The study transect is delimited by the two arrows. The insert shows the position of the Japtan reef in Eniwetok Atoll with wind direction indicated.

GENERAL PROCEDURES

During a six weeks' period at the Atomic Energy Commission Eniwetok Marine station a transect of quadrats marked by iron stakes was established on a relatively undisturbed and fairly typical inter-island reef shown in Figure 1. Many varied sampling procedures were combined to estimate the standing crop of the major component groups of the reef biota. Then chemical methods were used upstream and downstream to estimate the primary production and total respiratory metabolism of the reef. From these standing crop and productivity estimates, the turnover was obtained. Productivity data were combined with calculated light intensities to obtain an estimate of energetic efficiency.

In this approach it was imperative that a wide variety of methods be used all at the same time on the same area. Thus, fewer replications were made than would be required to obtain maximum accuracy from each method. Therefore it is the orders of magnitude which mainly emerge, but care is taken to base conclusions only on large, probably significant differences. Details of methods used are outlined in appropriate sections which follow.

The taxonomic composition of the reef community is tremendously varied from spot to spot whereas we believe the biomass per area is more constant. Weight estimates by trophic level based on our few quadrats are thus probably representative, but the quadrats should not be considered as population estimates by species. Many more quadrats would be required to estimate the densities of individual populations.

The 20 ft by 20 ft quadrat maps in Figure 5 were made in the field with pencil on acetate boards so that drawings could be made underwater using face masks.

Drs. R. W. Hiatt and M. S. Doty, who visited the reef, agreed with the authors that the quadrats mapped were fair samples regarding percentage of coral and general physiography.

THE WINDWARD REEF COMMUNITY,
ZONATION

The study reef (Fig. 1) is a part of the ring of submerged reefs which connects the small islands that make up Eniwetok Atoll. The transect is located 1/4 mile north of Japtan Island (Lady Slipper or Muti Island on some maps), on the eastern and windward edge of the atoll where the reef is 1500 ft wide (455 m). Most previous study transects of atoll reef communities have been made on island reefs where the water must break onto the reef and then return in the same path as an undertow. In contrast, this transect, like that of Sargent & Austin (1949), is across an inter-island reef where the water moves in only one direction from east to west with the wind; that is, from the open sea into the lagoon. On Eniwetok Atoll, the inter-island reef is actually the important predominant type.

As pointed out by Cloud (1954), many island reefs actually represent eroding reefs which were elevated above the water surface by a six-foot fall in ocean level which began at the end of the postglacial ther-

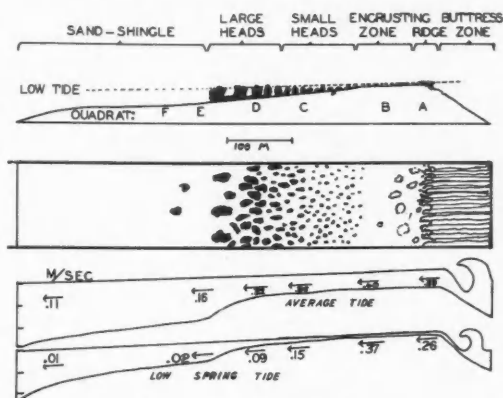


FIG. 2. Diagram showing the physiographic zones of the reef in surface and cross section view, and the average current velocities in m/sec. The approximate location of the 6 quadrats is indicated in the upper diagram.

mal maximum about 3000 years ago. These reefs are now in the process of being worn down. Only the front edge of present-day island reefs of Eniwetok support actively growing reef-building corals and algae, whereas many of the inter-island reefs support a vigorous community throughout. Consequently, the inter-island reef more nearly represents the "climax" or "steady state" community under present water level conditions. From the standpoint of productivity and metabolism it is quite clear that the inter-island reef is much more typical of an active coral community than is the half-dead, decadent island reef. These latter reefs, of course, may again become active when sufficiently worn down or if there is a future rise in sea level.

The transect of stakes was erected in a line parallel to the steady current traversing the reef. At no time during our observation were there tide pools with entirely stationary water. The zonation is very distinctive and apparently regulated by current velocities that decrease downstream as the depth increases. The descriptions of island reef zonation by Cloud (1952), Banner & Randall (1952), and Wells (1951) show very few similarities with the inter-island zonation on this reef, which is not surprising in view of points raised in the preceding paragraph. Tracey, Ladd & Hoffmeister (1948) class this type of inter-island reef as type IA.

As diagramed in Figure 2 and shown in aerial photographs and horizontal views in Figures 3-5, there are six physiographic zones as described briefly below.

WINDWARD BUTTRESS ZONE

The only information on the leading front of the reef comes from the aerial photograph in Figure 4 which shows the surge channels and buttresses running at least 200 ft (66 m) to seaward. It was not possible to sample this area because the algal ridge breakers could not be crossed.

Brief glimpses from a helicopter suggest that there is about a half coverage of coral in this zone.

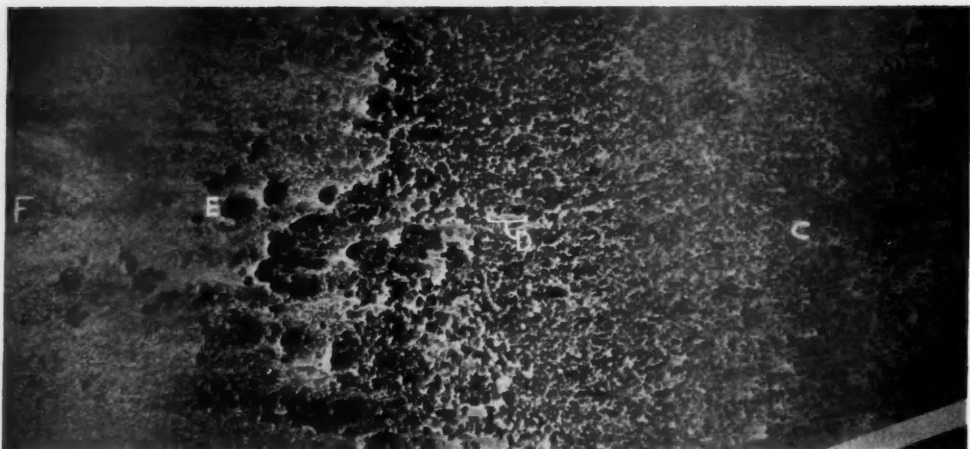


FIG. 3. Aerial photograph showing the zone of small heads (right one-third of picture), zone of large heads (center), and zone of sand-shingle of the down stream reef (left). Water flows from right to left. Zones of Quadrat C-F are marked.

Mayor (1925) found primarily species of *Acropora* in such an area.

CORAL-ALGAL RIDGE

In contrast to the massive algal ridges which have been described for windward reefs of Bikini and other atolls (Taylor 1950), the front ridge on the inter-island reef is a low, narrow ill-defined strip of limestone about 50 ft wide. The irregular surface is covered largely with corals and soft algae. The calcareous red algae (chiefly *Porolithon*), which are so prominent on Bikini reefs, are found mainly in small patches below the other algae or down in crevices. Our reef is an example of the principle (Tracey, *et al.* 1948; Ladd, *et al.* 1950; Cloud 1954) that inter-island reefs do not have so extensive an algal ridge or so elaborate a tunnel structure as do the island reefs. This is reasonable because the undertow on the inter-island reef is less on the front since much of the water goes over rather than back through. However, even the island reefs on Eniwetok have less calcareous superstructure than Bikini although much more than on our inter-island transect area. The lack of extensive superstructure may make the crossing of the algal ridge by a swimmer more difficult. The foam and combers on algal-coral ridges diminish the light penetration significantly and possibly cause the red algae to dominate.

The yellow encrusting *Acropora palmerae* (B-1),* small clumps of *Pocillopora* (A-1), and an encrusting form of *Millepora platyphylla* (B-2) are the chief corals which may cover up to half of the area of the ridge zone. Otherwise the ridge is covered with a thick mat of fleshy algae such as *Dictyosphaeria intermedia*, *Zonaria variegata*, *Ceramium*, *Dictyota*, and *Caulerpa elongata*. A characteristic feature is large purple sea urchins (*Heterocentrotus trigonarius*)

which wedge themselves into holes under the pounding surf. Rotenone sampling revealed a prevalence of small blennies and groupers. Sampling work on the ridge was possible only for a half hour during each low spring tide. The ridge is marked by white surf in Figures 1 and 4. Some idea of the distribution of coral and the much folded algal surfaces can be obtained in the diagram of Quadrat A in Figure 5.

ENCrustING ZONE

The first 200 ft (66 m) downstream from the ridge is a high, gently sloping plateau that at low spring tide is covered with only 6 in. of water. It is relatively the smoothest area with corals being either of a flat encrusting growth form or restricted to low rounded "heads" but little raised above the general reef surface. The range between tops of heads and ridges and the bottoms of depressions is only about one foot. As on the coral-algal ridge zone sheets of yellow *Acropora* and *Millepora* are conspicuous. In addition, there are scattered low, rounded heads of *Porites lobata* (B-6) and several species of favids (B-3, B-4, B-5). As shown in Figure 5, quadrat B, living coral colonies on these low heads are often crescent or doughnut shaped probably because the higher center portions are killed periodically by exposure during exceptionally low spring tides.

Filamentous red, brown, green, and blue-green algae form heavy encrusting mats over all of the zone which is not covered by coral, there being no areas of white sand as in the back reef zones. Small sea anemones are abundant, occurring in clusters throughout the algal mat. These belong to the genus *Actiniogiton* (Carlgren 1938), and apparently represent an undescribed species according to Charles E. Cutress who is currently working on this material. These anemones are remarkable in that they coat themselves with calcareous sand grains which are permeated with

* Code numbers refer to specimens deposited in the U. S. National Museum where final or more complete identification will be made when taxonomy of Marshall Island corals becomes better known.



FIG. 4. Aerial photograph showing the windward butresses on the east (right), the surf zone, the algal ridge (just to left of white line of surf), and the encrusting zone (left of ridge and covered with light-colored splotches of encrusting coral). Water leaving the zones pictured here flows downstream across zones pictured in Figure 3. Quadrats A and B are marked.

filamentous algae of the same type as found in the skeletons of corals.

Corals cover much less than half of the surface area (Fig. 5, quadrat B). From the air the zone has a wine-red color (algae) splotched with yellow (corals). The zone receives pulses of foam-water as the breakers throw rolls of water up on the plateau. Since there is a distinct slope the current is always strong even at low spring tide when the water pours steadily across like a broad mountain stream rippling over a rocky bed. Visual observation indicates that fish are not numerous in this shallow, rough-water zone, although schools of parrot fish were observed to cross the area and small fish were found in the few crevices which are available. The encrusting zone is visible just back of the line of breakers in Figure 4.

ZONE OF SMALLER HEADS

Fairly abruptly beyond the sloping plateau (encrusting zone) the water begins to deepen and the current diminishes accordingly. Coral heads become taller and more numerous but are still only a foot or so in diameter and height. The non-coral surfaces become lighter in color with less algal matting and more sand and more fragments of calcareous skeletons (rubble and shingle). As one moves downstream, the heads become larger and are coalesced into compound heads, often composed of several species. Quadrat C, Figure 5, is located near the lagoonward part of this zone. The numerous small heads and the formation of larger heads are well shown in this figure. Encrusting forms of *Acropora*, so prominent in the previous two zones, are absent. Massive, rounded heads of large calyx favids (C-2, C-3 *Favia pallida*, C-4, C-5 *Cyphastrea serailia*, C-7) reach maximum abundance in this zone. *Porites lobata* continues to be an important species, while colonies of the short, branching forms of *Acropora* first make their appearance in numbers (Figure 5). Large

branched *Acroporas* (*A. gemmifera*, C-10), which become more important in the next zone, are present in small numbers.

Small fishes are numerous in this zone and large fish come into the area when the current is not too strong. Two individuals of the poisonous stone fish, *Scorpaena gibbosa*, were found resting on the top of dead portions of heads when quadrat C was being mapped. So well did these fish blend with the background that one was at first sketched in as part of the reef structure before disturbance caused it to change its position!

The zone of small heads is well shown in the aerial photograph in Figure 3.

ZONE OF LARGER HEADS

As the water depth increases and the current becomes much less, the heads become massive compound structures, 2 to 4 ft or more in height and 2 to 20 ft in diameter, with channels of white sand and cobble floor in between the heads (quadrat D, Figure 5). Branching corals predominate, such as *Acropora gemmifera* (D-7), *A. cymbicrathus* (D-9), *Pocillopora*, *Stylophora*, and others, but massive types such as *Porites* and *Montipora* are present. There is a distinct *Millepora* zone composed of *M. platyphylla* (E-1) and the "stinging coral" *M. murrayi* (E-2) at the back edge of the zone of larger heads. The blue coral, *Helipora caerulea* (E-3), is fairly common, while large heads of *Turbinaria mesenterina* (E-4) represent the last important coral formations as one passes into the next zone in the lagoon. Quadrat D lies in the front part of the zone of large heads where *Milleporas* are less prominent.

Mounds of coral shingle (dead coral fragments, usually permeated with living filamentous algae) form the central mass upon which smaller live heads form wreaths. At low spring tide the branching type corals

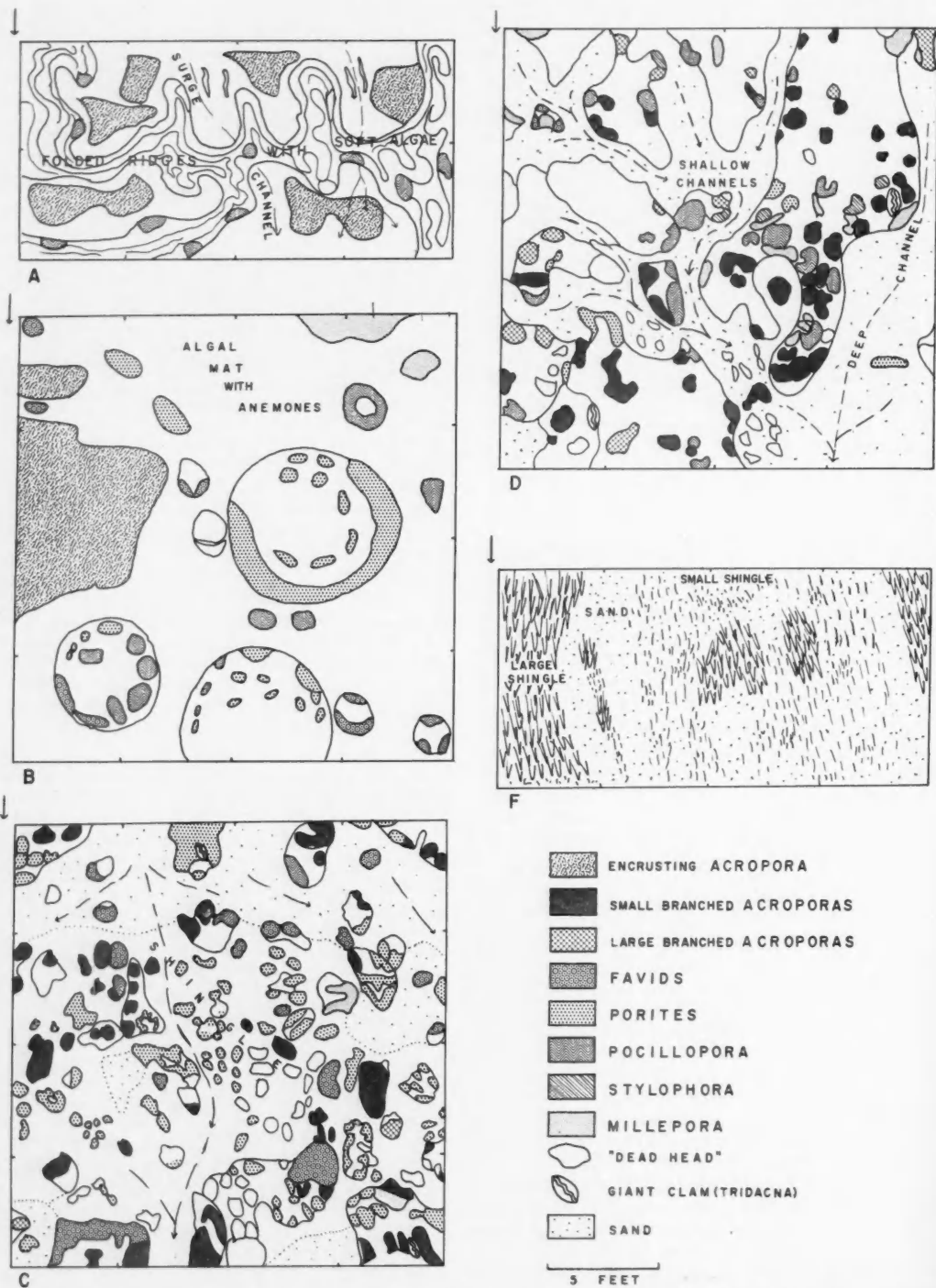


FIGURE 5. Quadrat maps showing distribution of corals and other major habitat features from front to back of the reef (see Fig. 2, upper diagram, for the approximate location of quadrats on the reef). Quadrat A, coral-algal ridge; quadrat B, encrusting zone; quadrat C, zone of small heads, quadrat D, zone of large heads; quadrat F, zone of sand and shingle.

on the tops of these compound heads break the surface, whereas the reef floor is 3 ft submerged. Swimming becomes easy in this zone. The majority of parrot fishes and surgeon fishes browse and school here. In superficial visual appearance, this zone is a beautiful jungle of live coral and fishes although as shown later, in terms of live protoplasm the plant world nevertheless dominates as usual. This zone as seen in Figure 3 is about 400 ft wide.

ZONE OF SAND AND SHINGLE

With gradually increasing depth and diminishing current, both the small and the larger coral heads, live and dead complexes, come to an abrupt end. A long flat shelf slopes lagoonward for 500 ft or more, covered with coarse and fine sand made up of fragments carried downstream from the front reef. Foraminifera of large types are abundant (Table 7). The fishes decrease except for the schools of sardine-like fishes that feed on the downstream drifting fragments of pseudoplankton and a few larger carnivorous fishes, including sharks, which cruise here. The area is predominantly white except for filamentous algae in the larger coral shingle fragments. Beyond the 500 ft of this long bare shelf there is a sharp steepening of slope for over 100 ft (33 m) down to the irregular lagoon floor. As seen from a helicopter the steepening of the slope is sharply marked by a border of the green turbidity of the lagoon water as the floor drops out of visible range.

The over-all change from the dark color of encrusting filamentous algae of the front reef to the white color of the back reef, where the filamentous algae are mainly within the dead and porous calcareous fragments, suggests a transition from a water-filtering source of nutrients up front to a sub-surface decomposition source of plant requirements on the back zone. It will be shown that the quantitative totals of over-all plant protoplasm per area are similar in order of magnitude.

CURRENT VELOCITIES

In the course of the study, 26 dye current measurements were made in different zones and time. Fluorescein dye (from air-sea rescue kits) was released into the water by one observer and the time required to travel a measured distance to a second observer was determined. The maximum current measured was 1.44 m/sec across the reef during a high water neap tide. Currents probably twice this velocity were encountered in incoming spring tides when the observers were too busy hastening to shore to get a measurement. The lowest velocity measured on the front reef encrusting zone was 0.18 m/sec; the lowest in the back reef lagoon shelf zone was 0.009 m/sec. The mean of eleven measurements on the encrusting zone was 0.49 m/sec. The 5 ft-deep water of high spring tides probably permits strong flow over the reef although no measurements were made at this time. The larger fish which are unable to hide behind small bumps and coral heads apparently could not browse on the middle reef when the current was run-

ning over 0.3 m/sec, for no larger fishes were observed in these zones at this time.

As a rough estimate of comparative and average currents, measurements made of water transport at a neap tide at one station are converted by calculation of depth effect into velocities for the different zones and reported in Figure 2. Currents change so rapidly with time in the tidal cycle that this is the only way to make a synoptic comparison. As indicated above it was difficult to obtain measurements during high water spring tide without being washed off the reef.

TROPHIC STRUCTURE

PLANT AND ANIMAL COMPONENTS IN LIVE CORAL; THE PREDOMINANCE OF PLANT PROTOPLASM

Early taxonomists classified corals as plants, as in John Ray's system (Nordenskiöld 1932), because of their vegetative appearance. Later, corals were found to be coelenterates and thus classified as animals. Yet their ecological roles that resemble plants remained a point of interest such as their predominance in the community and their practice of laying down carbonaceous substance in quantity sufficient to maintain the community substrate. Then, when the symbiotic zooxanthellae were found in the tissues of the animal polyp, it became evident that, metabolically, corals might be part-plant and contribute to the primary production of the community. Yonge, Yonge & Nicholls (1932); Kawaguti (1937); and others have shown that corals do indeed produce an excess of oxygen over carbon-dioxide during the daytime, although most measurements show that production does not quite equal respiration over a 24-hr period.

On ecological grounds, zooxanthellae, to match coral respiration, must either carry out photosynthesis many times faster than corals respire or exceed the coral animal protoplasm several times if a pyramid of mass should exist as required by the second law of thermodynamics for most systems. Yet corals have been shown to come close to achieving a balance between photosynthesis and respiration while possessing seemingly only a small amount of plant tissue in the form of scattered single algal cells restricted to the endoderm of the polyp.

However, there is yet a second plant component characteristic of corals, the significance of which seems to have been overlooked. When one breaks open a fresh, live coral head, conspicuous green bands are seen in the skeleton of the living polyp zone and also in the concentric layers in the older skeleton well below the zone of animal tissue as shown in Figures 6 and 7. These bands are not due to the yellow-brown, rounded zooxanthellae cells, but to a network of bright green filamentous algae growing in the pores of the inert skeleton (Fig. 7E). Although sometimes located as much as 2 or 3 cm below the surface, these algae growing within the translucent aragonite skeleton are, nevertheless, within light range of the intense penetrating tropical sun. All of the species of hard aragonite corals, examined at Eniwetok including hydrozoan, octocoral, and hexacoral groups contained

these filamentous green algae in abundance. Only *Dendrophyllia*, growing in the shade in Hawaii, was different in not possessing either the zooxanthellae or the filamentous greens of the skeleton.

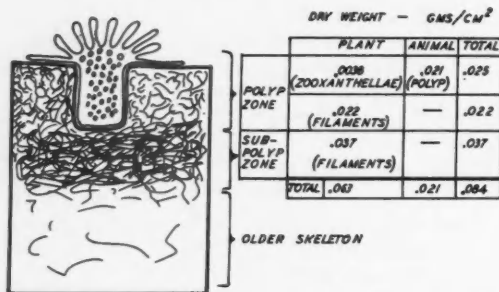


FIG. 6. Diagram in cross section showing the quantitative distribution of plant (algal) and animal (coral polyp) tissue in a generalized live coral head. Data on plant and animal biomass are from Table 4.

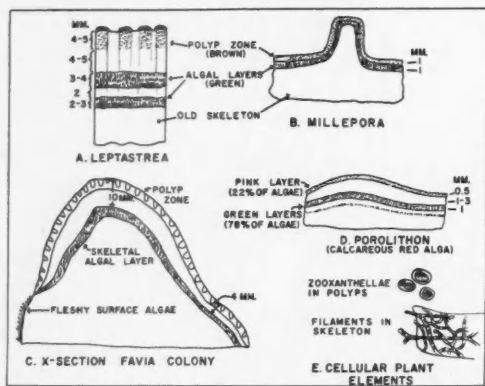


FIG. 7. Sketches from fresh material showing: A to C, the relation of the bands of skeletal algae to the polyp zone in three genera of corals. D, sub-surface green bands in the skeleton of calcareous red algae. E, the two major types of symbiotic plant material in coral colonies.

While zooxanthellae have long been considered symbiotic or mutualistic with coelenterate polyps, the possibility that the filamentous skeletal algae might also be symbiotic or at least important to the nutrition of the coral colony has been little considered. Indeed, most writers refer to these conspicuous algae as "boring algae" and consider them as parasitic agents which weaken the skeleton and hinder the growth of the coral colony. Duerden (1905) found two kinds of filaments, one with cross walls, one without. As one of the first to describe the filamentous skeletal algae, he stated that they "invade the corallum, weakening it if having no other effect." This view seems but little challenged although Edmondson (1929) stated that his evidence was not conclusive that these algae check the metabolism since he found that some "heavily infested" colonies showed good coral growth in the laboratory. It may well be, that

the boring filamentous algae of live corals are beneficial, and at least under conditions existing on this study reef, contribute to the survival and rapid growth of major reef builders. Thus, there is a sharp contrast between the boring algae in live corals and the different species boring in dead coral. The species of algae which have been described as boring in calcareous substrates are listed by Utseumy (1942).

The evidence that there is a predominance of producing plant protoplasm rather than coelenterate polyp protoplasm in a live coral head is based on high chlorophyll content found in the non-polyp parts of live coral heads relative to dry weight estimates of animal polyps. The dry weight of producing plant tissue was determined from the chlorophyll values with the graph in Figure 8 on the assumption that algae in the coral skeleton and polyps have a chlorophyll-dry weight ratio similar to free-living algae. Details of the method used are given below in the section on primary producers. Rough quantitative estimates of the dry weight of the animal-polyp component of a coral head were obtained by estimating the volume of the coral head occupied by polyps and assuming that the dry weight to volume ratio of anemones represents that of coral polyps. The polyp volume was estimated by a vaseline method. Further details on estimation of polyp volumes and dry weights are given in the section on coral polyps. Rough estimates of zooxanthellae dry weights were obtained from chlorophyll extraction of isolated polyps of a large polyp species (*Lobophyllia*) and from histological sections pictured by Yonge, Yonge & Nicholls (1931) and further described in the following section on producers. The data on plant and animal components are given in Tables 1, 2 and 4.

The estimate of .075 gm/cm² residue after treatment with 20% nitric acid (Mayor 1924) compares well with the finding of .062 gm/cm² mean loss on ignition (Table 2) as an estimate of total biomass.

The diagram in Figure 6 and the mean estimates of protoplasmic components in Table 4 summarize the data and present a general picture of the coral head, which is almost a whole ecological community in itself with producer, herbivore, and carnivore roles all in one. The essential components thus appear to be: (a) animal (non-photosynthetic) tissue, (b) zooxanthellae, (c) filamentous green algae in the sub-surface skeleton and between polyps, (d) bacterial components which are not estimated in this study but which may be of importance.

The important quantitative conclusion from Table 4 is that the total plant protoplasm exceeds the animal biomass (about 3 to 1) and the filamentous green algae have a greater biomass than the zooxanthellae (about 16 to 1). If the filamentous skeletal algae are considered an integral part of the coral colony along with the zooxanthellae, a reasonable biomass pyramid is obtained which is in line with the high photosynthetic activity shown by most coral colonies.

Comparison of live and dead corals provides indirect evidence of symbiotic relationship between

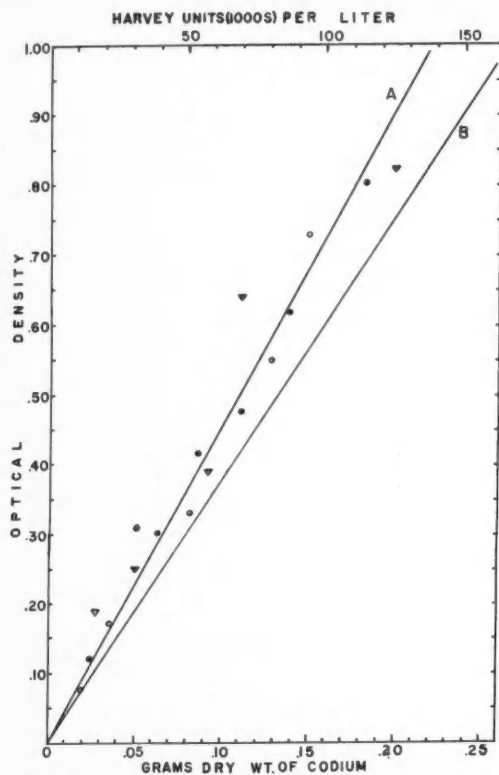


FIG. 8. Curve (A) relating chlorophyll to dry weight of *Codium edule*. This graph was used as a means of obtaining rough estimates of the dry plant protoplasm in coral heads and other calcareous substrates. The curve is based on three replications as indicated by the three types of symbols. B is correction for average loss of color on drying. See text for further explanation.

coral animals and filamentous algae in the skeleton. Algae occur in characteristic bands under living polyps (Figs. 6 & 7) and the bands show patterns which are characteristic for a given species. These sub-surface bands disappear if the coral animals above them died to be replaced by other algae which grow on and near the surface of the dead skeleton. Thus, the bands are not present on the sides of the head where there are no live polyps (Fig. 7C). Although no attempt was made to classify the filaments, the microscopic appearance of algae in bands under live polyps is clearly different from that of algae growing on and in dead coral material. Dead corals included boring greens, reds, and blue-greens, whereas the live corals observed contained only greens.

These observations suggest the hypothesis that skeletal algae, as well as zooxanthellae, have a symbiotic relationship with coral animals. Nutrients of coral metabolism may readily diffuse through the porous skeleton to the algae. The coral skeleton provides matrix and some enclosed nutrient, and the polyp-protoplasmic sheet on the outside protects the delicate filaments from competition, browsing, and

Table 1. Quantitative distribution of algae in corals.

	PERCENT OF TOTAL ALGAE		
	Polyp Layer	Sub-polyp Layer	
A. Vertical Distribution of Algae in Massive Corals			
<i>Leptastrea</i> sp. (B-3).....	40	60	
<i>Favia</i> sp. (C-3).....	34	66	
<i>Porites</i> sp. (B-6).....	40	60	
<i>Porites</i> sp. (B-6).....	46	54	
<i>Turbinaria mesenterina</i> (E-4).....	43	57	
Mean.....	41	59	
	PERCENT OF TOTAL ALGAE		
	In Branches	In Basal Zones	
B. Distribution of Algae in Branching Corals			
<i>Acropora</i> sp. (D-9).....	59	41	
<i>Acropora</i> sp. (D-9).....	57	43	
<i>Pocillopora</i> sp. (C-8).....	68	32	
<i>Lobophyllia</i> sp.....	66	34	
Mean.....	62	38	
C. Zooxanthellae in Coral Animal Tissue			
Percent zooxanthellae in a coral planula*.....		27%	
Percent zooxanthellae in a coral polyp (estimated from histological cross section)*.....		14%	
Mean of extraction of two <i>Lobophyllia</i> polyps.....		16%	
	Individual No. 1	Individual No. 2	Mean
D. Biomass Distribution in <i>Lobophyllia</i> , Gms/cm ²			
Biomass in Polyps:			
Zooxanthellae in polyps.....	.013 13%	.018 19%	.016 21%
Animal tissue in polyps.....	.041 97%	.077 81%	.059 79%
Total biomass of polyp.....	.054 100%	.095 100%	.075 100%
Comparison of Zooxanthellae and Algal filaments outside Polyps:			
Zooxanthellae in polyps.....	.013 31%	.018 18%	.016 19%
Algal filaments.....	.029 69%	.084 82%	.067 81%
Total plant biomass.....	.042 100%	.102 100%	.083 100%
Distribution of Plant Biomass:			
Zooxanthellae in polyps.....			.013 31%
Filaments around polyps.....			.015 36%
Filaments below polyps.....			.014 33%
Total plant biomass.....			.042 100%
Comparison of Animal and Plant Biomass:			
Animal biomass (from Table 4).....			.022 46%
Total plant biomass.....			.083 54%
Total plant and animal biomass.....			.155 100%

*Calculated from data of Yonge et al. (1931).

intense sunlight (note from figure 7C that algal bands are deeper in the skeleton at the apex where light intensity is greatest).

From the quantities of algae present relative to coral protoplasm, it would be supposed that coral animals benefit from diffusion of organic substances from the algae but direct evidence of this was not obtained. Coral animals would still need to obtain some food and critical nutrients such as nitrogen by ingesting plankton, since there is not enough plant material to completely support the coral and since the coral requires a higher nitrogen content. Also, it is possible that the sub-surface algae raise the pH

TABLE 2. Quantitative estimates of animal tissue in coral polyp zones gm/cm².

Species	Depth of Polyp Zone cm	Total Biomass (Loss on Ignition*)	Plant Biomass (Extract Methods; Tables 1 & 5)	ANIMAL BIOMASS IN Gm/cm ²			
				By subtraction (Total Minus Plants)	By Estimate of Polyp Volumes† (See Table 3)	By Direct weighing of isolated polyps‡	Mean Animal Biomass
<i>Pocillopora</i> (C-8).....	.1	.035	.036	-.001	.0015007
<i>Millepora</i> (B-2).....	.15	.044007007
<i>Porites</i> (D-2).....	.2	.043	.016	.027	.009018
<i>Heliopora</i> (E-3).....	.3	.0430144014
<i>Leptastrea</i> (B-5).....	.4	.062	.019	.043043
<i>Astreopora</i> (M-30).....	.5	.045015015
<i>Turbinaria</i> (E-4).....	.8	.062	.026	.036	.019027
<i>Favia</i> (C-3).....	1.0	.050	.019	.031	.029	.015	.025
<i>Lobophyllia</i>	2.2	.173	.081	.092	.064	.059	.072
Mean of corals.....	.64	.062025
Anemone-sand grain-algae complex.....	.5	.086034

*Loss on ignition in furnace at 600°C.

†Volume of polyp zone assumed to be filled with protoplasm like that of sea anemones growing on the reef with a density of about 1 and a 15.1% dry weight of wet weight. (Similar dry weights of wet weights are summarized for other Coelenterates by Vinogradov, 1953.) Estimates with 15% error of underestimation due to wet tissue in pores possibly cancelled by pore space occupied by plant filaments and zooxanthellae.

‡It is not possible to separate all of the polyp out, even in large polyp species. Possible compensation comes from using weights rather than loss on ignition of separated polyps.

TABLE 3. Density, porosity, loss on ignition of skeletons.

Species and Zone		Skeletal Density gm/cc	Gross Dry Density gm/cc	POROSITY IN % (vaseline method)			Loss on Ignition % (of dry)
				A	B	Mean	
FRESH DRIED LIVING CORALS							
<i>Pocillopora</i>	branch	2.09	1.86	10.0	12.4	11.2	4.9
<i>Millepora</i>	polyp zone	1.51	33.3	8.9
	whole	2.27	1.42	37.6
<i>Porites</i>	polyp zone	2.38	1.66	30.4	30.4	30.4	12.7
	Algal zone	1.98	1.50	17.4	26.5	22.0	4.7
	layer 3	2.08	1.70	15.4	21.0	18.2	4.5
	layer 4	2.33	1.72	24.4	26.0	25.2	4.4
	layer 5 (eroded)	2.24	1.68	20.1	32.2 (hole)	26.1	3.9
<i>Leptastrea</i> (B-3)....	polyp zone	2.38	1.82	23.3	4.1
	algal zone	2.28	2.12	7.0	2.6
	sub-algal	2.47	2.18	11.6	1.7
<i>Heliopora</i>	polyp zone	2.89	1.63	31.9	8.9
	whole	2.42	2.24	7.1
<i>Astreopora</i>	polyp zone	2.51	1.99	22.6	18.1	20.3	4.8
<i>Turbinaria</i>	polyp zone	2.44	1.90	22.0	4.5
	whole	1.50	38.7
<i>Favia</i> (C-3).....	polyp and algal zone	2.33	1.83	22.2	20.2	21.4	5.4
<i>Lobophyllia</i>	polyp zone	2.18	1.64	25.1	24.7	24.9	4.8
FRESHLY DRIED ALGAL SKELETON							
<i>Porolithon</i>		2.38	2.20	7.8	4.5
SKELETONS FROM REEF MASS, 20 FT DEEP IN DYNAMITE HOLE							
<i>Porolithon</i>		2.64	2.53	3.2	3.9
<i>Favia</i> ?.....		2.38	2.22	6.7	2.9
MEAN OF POLYP ZONES (7).....							
		2.44	1.73	26.6	7.0
MEAN OF SUB-POLYP ALGAL ZONES (2)...							
		2.13	1.81	14.5	7.3
MEAN OF SUB-ALGAL LAYER ZONES (3)...							
		2.29	1.87	18.3	3.5

TABLE 4. Summary of components of biomass in corals, mean data. Figures given: in gm/cm² dry weight and in percent of total biomass.

		Plants Tissue	Animals Tissue	Total Biomass
Polyp Zone	In Polyps	.0038* (zooxanthellae) 4.5%	.021† 25%	.025 30%
	Between Polyps	.022‡ (filaments) 26%022 26%
	Total in Polyp Zone	.026‡ 31%	.021 25%	.047‡ (.062§) 56%
Sub-polyp Zone		.037** (filaments) 44%037 44%
Total Biomass Outside Polyps		.059 70%059 70%
Total of all Layers		.063†† 75%	.021 28%	.084 100%

*Mean of zooxanthellae extracted from *Lobophyllia* (13% and 15% of polyps in Table 1) and calculated from Yonge (14% of polyps in Table 1). 15.3% of 0.25 gms/cm² polyps (from Table 2).

†.025 gms/cm² polyps (from Table 2) minus zooxanthellae estimate .0038 gms/cm².

‡Total plant estimate for the polyp zone minus zooxanthellae estimate.

§14% (from Table 1) of Plants are in Polyp zone; mean plant estimate per area of coral .063 gms/cm² from Table 5.

||Sum of plants and animal estimates.

**Total organic matter estimate based on loss on ignition at 600°C for comparison. (from table 2)

***59% of plants in sub-polyp algal zone (from Table 1); mean plant estimate per area of coral .063 gms/cm² from Table 5.

††From Table 5.

(and thus slow skeletal decomposition) or actually contribute directly to the skeleton formation of the coral complex. Certainly evidence is lacking that the presence of algae in any way weakens the live skeleton so long as the coral-algal complex is intact. The high strontium content of aragonite coral skeletons being in the same or higher ratio to calcium as the sea water (9.23 atoms per 1000 atoms) is unusual for calcareous animals. The similar high ratio in the green calcareous alga *Halimeda* suggest some similarity in the deposition process of corals and *Halimeda* that might be explained by a role of the green filamentous algae in deposition in the coral. Since the green filaments are tightly enclosed within the coral colony, any organic matter produced by them as growth or surplus diffusible products cannot escape without going through the enclosing polyp zone. There is no room for such growth except as the whole colony grows and there is no visible accumulation of organic products. The situation leads to the supposition that either the plants are growing close to the compensation point or are supplying coral animal polyps with organic materials. Since there are often several bands of healthy green filaments, it is possible that, if the deepest band were at the compensation point, the top bands would be making an excess which was being used by the corals and deeper algae.

From the standpoint of the entire reef ecosystem it does not matter how much food made by algae within the live coral head is used by coral animals directly. Only by considering the large amount of producer tissue in a coral head is it possible to explain the



FIG. 9. A positive print of an autoradiogram of a section of a coral head (*Goniastrea*) after two days' exposure; light areas indicate exposed and dark areas unexposed film. Note that the surface polyp zone, but not the subsurface algal bands (see Fig. 7), exhibited considerable radioactivity.

great preponderance of organisms classed as animals. Thus the coral reef is like most known self-sufficient ecosystems in having a much greater weight of plant biomass than animal biomass.

An internal use and reuse of nutrients in a living coral is suggested by the autoradiogram (positive) in Figure 9 which is typical of ten made from corals from the generally (low level) radioactive Japian reef. The radioactivity is entirely restricted to the animal polyp zone. Whereas algae on dead reef surfaces were intensely radioactive, these forms beneath the corals are apparently not in nutrient contact with the outside water except through the coelenterate tissues. This may be interpreted as an evidence that

the coral algal filaments receive nutrients from the corals. By this view the radioactive elements in the polyps are not of the type which are released by the corals during their daily metabolic cycles. Cerium and praeosodmium have been strongly implicated as main components to previous reef radioactivity (Blinks 1952; Donaldson *et al.* 1950). Apparently the calcophile elements like calcium and strontium are not retained but rapidly exchanged away by the high non-radioactive concentrations in the flux of sea water over the reef.

Although the filaments and zooxanthellae are small in size, their photosynthetic rates on a dry plant weight basis (Mayor 1924) are not nearly as high as free algae growing in nature as quoted by Verduin (1952); thus, for the same production per area, more biomass is required than in a plankton population, for example.

If the filamentous algae are truly mutualistic with corals then there may be no need to create separate taxonomic names for them. The coral-algal complex could be considered as a single species entity as is the fungal-algal complex of lichens, and the established names for the corals used to cover both elements.

PRIMARY PRODUCERS

In the previous section the complex association of plants and animals in a live coral head was discussed with a new viewpoint. In this section all of the main groups of primary producers (plants) are described and quantitative estimates are presented in Table 5.

The main primary producers grouped ecologically are as follows:

- (1) filamentous algae in live corals.
- (2) zooxanthellae in coral polyps.
- (3) algae matted as an encrustation on and in the dead rigid porous reef substrate surface in the swift current zone.
- (4) Encrusting fleshy green types such as *Dictyosphaeria*, *Zonaria*, and *Caulerpa* attached to the irregular surface, with encrusting calcareous reds such as *Porolithon* and *Lithophyllum* mostly beneath.
- (5) Small algae in and on loose coral shingle (broken coral pieces) lying in channels and in areas between coral heads.
- (6) Small filamentous algae in and on "dead heads." (A dead head is defined as a coral formation no longer containing living coral polyps but still standing erect on the surface of the reef.)
- (7) Large conspicuous bunches of branching algae attached around dead heads including genera such as *Codium*, *Asparagopsis*, and *Halimeda*.
- (8) Algae in the coarse, white, calcareous sand which covers inter-coral areas of the back reef.
- (9) Zooxanthellae and filamentous algae in animals other than coral polyps such as sea anemones and giant clams (*Tridacna*, etc.).
- (10) Planktonic algae derived from the open sea and the much larger quantity of pseudoplankton breaking off the other sessile masses. Sargent & Austin (1949) showed the relative insignificance of the plankton production in the reef's metabolism.

The relative sparsity of true plankton is suggested by the absence of attached plankton feeding molluscs, hydroids, tunicates, and ectoprotecs on the glass slides as reported in Table 6. The attachment aufwuchs was entirely autotrophic.

A reef community resembles a complex, tropical, terrestrial community in that it is not dominated by one or two producer species, but there is considerable diversity and variation from place to place. On the reef, for example, the myriads of tiny blue green,

TABLE 5. Primary producers of the reef.

1. ALGAE IN LIVING CORALS (filaments in skeleton and zooxanthellae in polyps)	Quadrat	Gms. Dry Wt. per cm ²
(a) Massive Scleractinia		
<i>Leptastrea</i> (B-3).....	B-C B-C B-C B-C B	0.049 0.038 0.049 0.037 0.033 0.076
<i>Favia</i> (C-3).....	B-C B-C B-C	0.054 0.060 0.058
<i>Favia</i> (B-4, green species).....	B-C C	0.116 0.135
<i>Pcrites lobata</i> (C-1).....	C-D C-D B	0.044 0.040 0.043
<i>Porites lobata</i> (in deep water).....	E	0.016
<i>Turbinaria mesenterina</i> (E-4).....	E	0.060
<i>Acropora palmerae</i> (B-1, encrusting form).....	B	0.036
Mean of Massive Scleractinia.....	..	0.056
(b) Branching Scleractinia		
<i>Acropora cymbicathus</i> (D-9).....	D D	0.038 0.048
<i>Pocillopora</i> (C-8).....	C C A	0.077 0.038 0.043
<i>Lobophyllia</i>	* *	0.124 0.053
Mean of Branching Scleractinia.....	..	0.060
(c) Octocorallia and Milleporina		
<i>Heliopora caerulea</i> (E-3).....	D	0.056
<i>Millepora platyphylla</i> (B-2), encrusting section.....	D	0.029
vertical branch.....	E	0.094
<i>Millepora murrayi</i> (E-2), encrusting section.....	E	0.078
encrusting section.....	E	0.080
encrusting section.....	E	0.065
encrusting section.....	E	0.041
vertical branch.....	E	0.117
vertical branch.....	E	0.074
Mean of Octocorallia and Milleporina.....	..	0.070
Mean of all corals (33 specimens, 12 species).....	..	0.063

TABLE 5. Primary Producers of the Reef (Continued).

2. ALGAE IN REEF SUBSTRATES	Quadrat	Gms. Dry Wt. per cm ²
Reef floor—with fleshy algal mat.....	A	0.062
Reef floor—with fleshy algal mat.....	A	0.041
Reef floor— <i>Porolithon</i> encrusted.....	A	0.042
Reef projection, upper plus under surface	A	0.092
Reef projection, upper plus under surface	A	0.080
Reef floor—with fleshy algal mat.....	B	0.072
Reef floor—with anemones on surface....	B	0.070
Reef floor—very porous.....	C	0.122
Algal mat separated from reef surface....	B	0.008
Algal mat separated from reef surface....	B	0.007
Algal mat separated from reef surface....	C	0.004
Algal mat separated from reef surface....	C	0.003
<i>Porolithon</i> separated from reef surface....	A	0.030
Rubble (Shingle), new, non-porous.....	C	0.029
Rubble (Shingle), old, porous.....	C	0.047
Rubble (Shingle), old, porous.....	D	0.066
Rubble (Shingle), old, porous.....	D	0.060
Rubble (Shingle), old, porous and eroded.....	D	0.141
Rubble—buried 25 cm deep in dead head	D	0.028
Rubble (Shingle), old, porous.....	F	0.110
Deadhead—surface and internal algae....	D	0.049
Deadhead—internal algae only, surface "grazed" by fish.....	D	0.042
Deadhead—.....	D	0.061
Deadhead projection, upper plus under surface.....	D	0.160
Sand—deep channel.....	D	0.0019
Sand—shallow channel.....	D	0.017
Sand—deep channel.....	F	0.009
Mean—reef floor.....	A-C	0.073
Mean—old shingle.....	C-F	0.085
Mean—deadheads.....	D	0.078
Mean—sand.....	D-F	0.009

3. ALGAE IN ANIMALS OTHER THAN CORALS	Quadrat	Gms. Dry Wt. per cm ²
Anemones—sand complex; zooxanthellae in polyps and filamentous algae in attached sand grains.		
Sample 1—zooxanthellae in polyps plus filamentous in attached sand....	B	0.037
Sample 2—zooxanthellae in polyps plus filamentous in attached sand....	B	0.025
Sample 3—zooxanthellae in polyps only filamentous in attached sand.....	B	0.030
	B	0.017
Total.....	B	0.047
Sample 4—zooxanthellae in polyps only filamentous in attached sand.....	B	0.045
	B	0.019
Total.....	B	0.064
Giant clam (<i>Tridacna</i>)		
Algae in mantle exposed to sun when shell fully open.....	D	0.052
Algae in calcareous shell of same specimen.....	D	0.031

*From lee reef at Rigi Island

TABLE 6. Reef fouling on glass slides submerged 21 days. (Each figure unless otherwise indicated is the mean of 5 counts; slides submerged July 3 to July 24, 1954; counts in numbers of individuals per cm².)

	Front Reef Encrusting Zone	Back Reef Zone of Large Heads	Slides imbedded in coarse bottom sand
Station designation (quadrat).....	B-1	D	C
Depth of water over slides at low-water spring tide in cm.....	10	30	20
Larger algae (greater than 5 microns) individuals/cm ² :			
Greens (<i>Enteromorpha</i> , siphonaceous)....	97	33	0
Browns (<i>Ecocarpus</i> and others).....	290	53	133
Reds (filaments and calcareous pieces)....	2	26	0
Blue-Greens.....	47	39	3
Diatoms.....	0	693	20
Smaller algae (less than 5 microns)			
Greens.....	1.2 x 10 ⁵	9.0 x 10 ⁵	15.4 x 10 ⁵
Blue-Greens.....	2.4 x 10 ⁵	.2 x 10 ⁵	6.6 x 10 ⁵
Encrusting diatoms.....	52.8 x 10 ⁵	5.4 x 10 ⁵	.4 x 10 ⁵
Bacteria.....	4.4 x 10 ⁸	2.4 x 10 ⁸	1.2 x 10 ⁸
Ciliates, nematodes, other similar sized soft bodied animals.....	600	132	15
Foraminifera (small sized types).....	.6	.4	0
Dry weight of algal protoplasmic biomass by chlorophyll method in mg/cm ²	2.5	1.6	..
Plankton feeders such as barnacles, molluscs, ectopods, hydroids, tunicates	0	0	0

brown, red, and green algal filaments embedded in live and dead calcareous materials have been little studied, yet they make up a large part of the food making biomass of the reef community. Some idea of this component can be gained from counts of attached algae on glass slides (Table 6). In spite of the great diversity in species there seems to be a fairly uniform distribution of producer biomass as estimated with the chlorophyll method. Particularly since the living primary producers are so completely interwoven with animal material and in dead skeletal material, the chlorophyll extracting method seemed to be the most practical way of obtaining quantitative estimations readily comparable with other communities. To permit comparison with other areas the chlorophyll methods are outlined in some detail. It is recognized that chlorophyll is not a perfect measure of the active plant protoplasm and that it varies considerably with species, physiologic age, and growth conditions.

All values for irregular shapes are reported in gms dry weight per area of the horizontal plane covered. (This surface is much less than the surface area of the irregular object.) For corals a small block was cut out with a hacksaw and the area of the block's projection on the horizontal surface was measured. The block was cut deep enough to include all visible green material (25 mm usually sufficed for massive corals, deeper sectioning was required for branching forms). It was later found that some algae occur even below the visible green zones but the amount is so small as to be scarcely measurable with the methods used. The block was pulverized with a

hammer, ground up in a mortar and extracted with successive washings of acetone until all the chlorophyll had been removed. The extract was filtered into a test tube, adjusted to 20 ml and read photometrically. Reef substrates, rubble and dead heads were also cut into blocks with a measured surface area and treated in the same way, care being taken not to lose the algae growing on the surface. Sand from a measured area was removed into a bottle and then ground and extracted in the same manner. It was found that materials must be extracted fresh, preferably not more than 12 hours after collection. Oven-dried materials invariably gave lower values than comparable fresh materials. For corals and most reef materials a piece with a surface area between 1 and 4 sq cm was required for extraction with 20 ml of acetone.

In the massive corals, algae are concentrated in layers just beneath the surface (Fig. 7) while in branched corals it is distributed along the branches with less concentration at the base and with relatively little at the exposed tips of branches. In fact in some branched forms the algae are so diffuse that the intensely green solutions derived from pale pieces of coral are surprising. A "block" of a branching coral type such as *Aeropora* or *Pocillopora*, as used for extraction, consisted of a vertical branch together with the basal section from which the branch arose. The cross sectional surface area of such a block (including all branches in the imaginary prism directly above the measured area on the horizontal) was considered comparable with the surface area of flat encrusting corals, since the amount of light per square centimeter of horizontal surface should be similar.

To convert photometric readings into biomass of producing tissue, a calibration curve was determined from acetone extracts of known dry weights of an arbitrarily chosen alga abundantly available in the field. *Codium edule* was selected as a standard and a relatively constant relation was found between chlorophyll content and dry weight (Fig. 8). A small portable colorimeter was used at first until a Coleman Spectrophotometer Model 6 became available. *Codium* used for calibration was freshly collected and paired, duplicate pieces were respectively dried and extracted for chlorophyll. Since a 20% loss of chlorophyll was found in pieces oven dried at 100° C for 6 hr, all extractions based on oven dried materials must be corrected for loss on drying. Figure 8 shows the calibration curve for optical density at 670 millimicrons as a function of *Codium* dry weight based on 3 replications on 3 different batches of material. A straight line results with monochromatic light. With the colorimeter first used, a reproducible curved line was obtained for absorption as a function of dry weight of *Codium*. The line allowing 20% correction for loss of chlorophyll on drying is also drawn in Figure 8. A series of nickel-chromium solutions was made as reference standards and readings equivalent to dry weights of *Codium* were included in Figure 8 (upper scale). 10,000 Harvey units/l were made up with 4.3 gm/l nickel sulfate and .25 gm/l potassium dichromate. Since the readings reported in Figure 8

were made with a spectrophotometer as 670 millimicrons instead of visually as originally defined (Harvey 1934), these are not Harvey units as usually used as a measure of chlorophyll but considerably different. Measurements made later on the nickel-chromium solution with a Beckman model DU spectrophotometer indicate that the optical densities in Figure 8 were made with an optical path of about 2 cm. From Richards (1952) these densities indicate an order of magnitude of .7 mg chlorophyll/gm dry *Codium*.

The values for algal dry weights obtained with the above methods are given in Tables 1 and 5 arranged according to the general producing types previously listed. These dry weights may be overestimates since the small filamentous strands, so important in many reef materials, are smaller and thus likely to have a lower dry protoplasmic weight-chlorophyll ratio than that characteristic of the standard used, *Codium*. No correction was made for ash in *Codium*.

The following tentative conclusions are indicated from these data about primary producers:

1. There is a striking similarity between values obtained with different species of corals. When expressed in terms of cross-sectional area projected on the horizontal, the branching types as compared with flat or rounder massive types were little if any higher in algal content even though much more calcareous matter was extracted and even though the actual surface area of branching forms exposed to the water was much greater. The branching life-form may be an advantage to the animal part of the coral in catching plankton from deep water and possibly useful to plant components in obtaining nutrients. The functional plant producers, however, seem to be regulated by the available light and are more widely dispersed in the branching forms. Thus, in general, the chlorophyll, per area perpendicular to the sun, is surprisingly uniform. The chlorophyll per area of a steady-state community may be expected to have a uniformity and greater significance than in transient bloom populations and laboratory cultures. It may be a better measure of producers and productivity under these more constant conditions.

2. While the algal content of different species of corals was of the same general order of magnitude, distinct species differences are indicated. Thus among the massive corals an unidentified species of *Favid* (code #B-4) had about twice the algal content of other species of *favids* (Table 5). This coral is very green in appearance with abundant green algae and zooxanthellae in the surface in the polyp zone as well as in the subsurface zone. Among the branching types, *Millepora* appears to be high and in both species (*M. platyphylla*, *M. murrayi*) the tall vertical branches were found to contain more algae per cm² cross section than flat portions of the same colony. A wide 100 fold range of production and respiration values had been established for corals by Kawaguti (1937).

3. In so far as our small number of samples shows,

there was little evident difference in producer content of live corals in different zones of the reef which range from $\frac{1}{2}$ to 4 ft deep at low spring tide. Similarly, the corals collected in Kaneohe bay in Oahu, Hawaii although from more turbid water gave similar orders of magnitude of chlorophyll content for comparable species.

4. The white sand area of the back reef was the only major area of the reef which had a definitely lower biomass of producer protoplasm.

5. From the data on glass slide attachment in Table 6, about twice the growth of encrusting algae was obtained in the front reef as on the back reef correlating with the predominance of encrusting forms up front with boring forms in back.

CORALS AS CONSUMERS

Estimates based on mapped quadrats (Figure 5) indicate, along with cursory survey, that most of the reef surface is between 16% and 50% covered with live coral. Although the living part of a coral is more plant than animal there is, nevertheless, an important total weight of animal coral. It has been repeatedly shown (Mayor 1924, Edmondson 1929, Yonge 1930) that coral polyps are in part carnivores in trophic classification, since they catch zooplankton, especially at night. And if the inferences of the previous sections and of previous authors (reviewed in Yonge 1930, Kawaguti 1937) are correct, a coral animal polyp is very much an herbivore because of nutrition received from symbiotic algae. Thus, the animal part of a coral is partly divided in trophic classification between two trophic levels, herbivores and carnivores. Three procedures were used to obtain an estimate of the dry weight of the consumer fraction in live coral.

First, the volume of the polyps was estimated by filling the pores of a slice of coral from the polyp zone with melted vaseline. From the amount of vaseline filling the pores, the polyp zone porosity is determined as an upper limit to the polyp volume. One source of error, the inclusion of pores not occupied by polyps, may be cancelled by the error of not including pores partly blocked by animal and plant dry-residues. In drying, shrinkage of polyps may be expected to be greater than shrinkage of algal filaments within the skeleton. Thus, a rough upper limit figure for primarily animal volume (with enclosed zooxanthellae) may be obtained. The steps in this procedure are as follows: (1) cut a slice of polyp zone with hacksaw, measure surface area, dry, and weigh; (2) place in melted vaseline in oven 6 hours until permeated, remove, cool, wipe all excess vaseline off the outside, weigh; (3) the figure for vaseline in pores obtained by subtraction of weights, should be divided by the density of the vaseline to obtain the volume occupied; (4) multiply the volume by the dry weight equivalent for anemones and divide by the area to obtain final figure for dry weight polyp per square centimeter.

For two species with large polyps, it was possible

to tease out the protoplasm and obtain a dry weight directly.

In the procedure for the third method of estimating polyp biomass, the chlorophyll-based estimate of the plant part of the polyp zone is subtracted from the total loss on ignition (600°C). This method assumes that most of the loss on ignition of the polyp zone is due to ashing of live plant and animal tissues.

Some estimates for polyp weights from the three methods outlined above are given in Table 2, where they are in sufficient agreement to permit some confidence in the order of magnitude at least. The predominance of plants over the animal component seems clear.

The role of current in limiting coral distribution is supported by their distribution relative to currents at low tide (Fig. 2). Values for the quadrats show a decrease in coral coverage as the current decreases. Since ample light for photosynthesis penetrates the clear waters of the back reef it would seem likely that current is a major factor in the decrease of coral coverage.

CONSUMERS OTHER THAN CORALS

Although the trophic relationships of most of the higher organisms on the reef are very imperfectly known, an attempt has nevertheless been made to make rough groupings by trophic level as to herbivores, carnivores, and decomposers. Drs. Hiatt and Weylander generously gave their help on this, drawing on studies of food relationships in preparation.

Each of the groups required a suitable means of obtaining a weight estimate per area. It must be realized that the great clarity of water permits face mask work with as great visual intimacy as on a terrestrial quadrat. In Tables 7-12 are presented the results of the various estimates by methods briefly listed with trophic levels below. Where an organism eats the matting of algae with included small invertebrates, an omnivore classification might be correct except that by weight most of this material is plant. So, such consumers are classed as herbivores. For example, a negligible biomass estimate was obtained for microcrustacea in algal mats.

The following are the groupings and methods used for estimating trophic components. Since considerable doubt exists as to the trophic relationships, the groupings are kept separate in the presentation to

TABLE 7. Benthic Foraminifera; counts of individuals/cm². (Counts of representative algal mats and sand patches have been multiplied by the coverage of these areas in the quadrats.)

Quadrat	Coverage of sands or mats containing Foraminifera	Small Forams .01 cm size	Large Forams .1 cm size
B (Front, encrusting).....	70%	25	0
C (Small Heads).....	34%	2	5
D (Large Heads).....	34%	2	32
E (Sand-Shingle).....	67%	3	54

TABLE 8. Dry biomass estimates on quadrat A on the algal-coral ridge.

Biomass Component	Quantity measured, calculation	Mean Biomass averaged over the Quadrat gms/m ²
PRODUCERS		
Algae in corals	Coral coverage estimated 50% (Fig. 5) Algae in non branching coral .063 gms/cm ² (Table 5).....	315.
Fleshy and calcareous Algae in crust and subcrust	Algae coverage estimated 50% (Fig. 5) .064 gms/cm ² (Table 5 average Quad. A reef floor).....	320.
Total Estimate of Producers.....		635.
HERBIVORES PREDOMINATELY		
Slate per. cil urchins (<i>Heterocentrotus trigonarius</i>)	Quadrat count: 6(5, 5, 8) individuals/9 m ² 50.3 gms loss on ignition/individual.....	39.4
Gammarids and other small crustacea	Mean of 2 methods A. 16 individuals/9 cm ² ; .0004 gms loss on ignition/individual..... B. .086 gms/.04 m ² collected sample.....	4.7
Animal tissue in corals (partly carnivore but classed as predominately herbivore because of symbiotic algae)	50% coverage (Fig. 5); .021 gms/cm ² (Table 4).....	105.
Parrot fish	Visual counts: .4 individual/28 m ² ; 9.3 gms loss on ignition/individual.....	0.1
Total Estimate of Herbivores.....		149.
CARNIVORES PREDOMINATELY		
Annelids, mostly of Nereid type	.65 gms/.04 m ² sample.....	16.1
Small crabs and other similar sized crustacea	.28 gms loss on ignition/.04 m ²	7.
Total Estimate of Carnivores.....		13.1
Total Biomass.....		807.
H/P .24; C/H .09.		

permit rearrangements as further knowledge becomes available.

HERBIVORES

Small herbivorous fishes, including primarily surgeons and damsels, were counted on the 20 ft quadrats visually and converted to dry weight using the mean dry weight per fish found in a rotenoned sample. A similar method of visual census of coral reef fish has been recently described by Brock (1954). Three species, namely, *Acanthurus elongatus*, *Pomacentrus jenkinsi*, and *P. caudli*, made up a large percentage by weight of small herbivorous fishes at quadrat C and D as shown by rotenone samples.

Large herbivorous fishes, including especially surgeons, damsels, parrot fish, and butterfly fishes were rapidly counted with 360° underwater vision. The area of this sample was estimated from horizontal visibility measurement, and the dry weight per fish

Table 9. Dry biomass on quadrat B on the encrusting zone.

Biomass Component	Quantity Measured, basis for calculation	Mean Biomass averaged over the Quadrat gm/m ²
PRIMARY PRODUCERS		
Slab of reef rock surface containing substrate boring algae and mats of encrusting algae	70% coverage; (Fig. 5) Chlorophyll extract estimate: .072 gm/cm ²	804.
Slab of reef floor covered with anemone-algal permeated grain complex	Coverage 7.0%; chlorophyll extract estimate .070 gm/cm ²	49.
<i>Halimeda</i> clumps	Coverage 1%; .036 gm/cm ² loss on ignition of clump.....	4.
Algae in corals	Coverage of corals 22% Mean biomass of algae in non-branching corals. .063 gm/cm ² (Table 5).....	139.
Total Estimate of Primary Producers.....		696.
HERBIVORES PREDOMINATELY		
Animal tissue in corals (partly carnivores; classed as herbivore due to symbiosis with algae)	Coverage of corals 22% (Fig. 5) .021 gm/cm ² animal tissue in coral (Table 4).....	46.
Snails (<i>Thais</i>)	Counts: 16.5 (16, 17) individuals/1.44 m ² ; .094 gm dry tissue/individual.....	1.
Sedentary annelids in reef floor	Visual count: 65/1.44 m ² of non coral area; 70% coverage; .12 gm dry/individual.....	4.
Cucumbers	Count: 3/36 m ² ; 2.4 gm/indiv. loss on ignition.....	.2
Parrot fishes	.4 individuals/28 m ² ; 9.3 gm loss on ignition/individual.....	.1
Ophiroids in coral heads	Coverage of suitable heads 8.6%; 1.59 gm loss on ignition in sample head .04 m ²	3.4
Anemones (also carnivores; partly herbivores because of symbiotic algae)	.043 gm loss on ignition/individual 7.0% coverage of anemone complex; 17 individuals/120 cm ² of anemone area.....	4.3
Total Estimate of Herbivores.....		59.0
CARNIVORES PREDOMINATELY		
Nereid type annelids in coral heads	Coverage of heads 8.6%; 1.86 gm loss on ignition/.04 m ² head.....	4.
Small crustacea, crabs in coral heads	.22 gm loss on ignition/.04 m ² ; coverage of heads 8.6%.....	.5
Total estimates of carnivores other than corals and anemones.....		4.5

was determined from a sample of 12 speared fish of the same general size. *Scarus sordidus*, *S. erithronus*, *Chaetodon auriga*, *C. ephippium*, *C. trifasciatus*, *Centropyge flavissimus*, *Naso lituratus*, *Acanthurus olivaceus*, and *Ctenochaetus striatus* were important species in this group.

TABLE 10. Dry biomass estimates on quadrat C on the zone of smaller heads.

Biomass Component	Quantity Measured, basis for calculation	Mean Biomass averaged over the Quadrat gm/m ²
PRIMARY PRODUCERS		
Algae in live coral	Coverage of coral 19% (Fig. 5) .062 gm/cm ² dry algae in coral (Table 5)...	118.
Coral shingle permeated and encrusted with algae	Coverage of shingle 47%; .038 gm/cm ² dry algae in shingle.....	178.
Algae in and on hard reef floor	Coverage of algal encrusted floor-rock 23%; .122 gm/cm ² dry algae.....	286.
Algae in and on small dead-heads (Quadrat C dead-heads like reef floor in respect to algae)	Coverage of dead-heads 11%; .122 gm/cm ² dry algae.....	134.
Giant clam algae	.2% coverage; .052 gm/cm ² of exposed mantle photosynthetic surface...	1.
Total Estimate of Producers..		717.
HERBIVORES PREDOMINATELY		
Small cucumbers in dead-heads	3 individuals/0.26 m ² of head; 2.4 gm loss on ignition/individual; 11% coverage of dead and live coral heads..	31.
Small cucumbers around corals and in shingle	20 individuals/18 m ² ; 4.8 gm loss on ignition/individual.....	5.3
Large cucumbers	14 individuals/18 m ² ; 17.7 gm loss on ignition/individual.....	14.
Small urchins in dead heads (<i>Echinothrix</i>)	1.01 gm (4 individuals) loss on ignition in 260 cm ² ; 11% coverage of dead heads	4.2
Large urchins (<i>Echinothrix</i>)	56 individuals/18 m ² ; .61 gms loss on ignition per individual.....	1.9
<i>Tridacna</i> (small) (herbivorous because of symbiotic algae)	3 individuals/36 m ² ; 12.7 gm dry/individual minus 1 gm /m ² plant in clam (see above).....	.1
Annelids in dead heads	20 gm dry (19, 21)/100 cm ² dead head; 11% coverage of dead heads; loss on ignition 57%; 70% herbivores..	9.0
Sedentary annelids on hard reef floor	.126 gm loss on ignition/30 cm ² of reef flat; coverage 23%.....	10.4
Sponges	10 cc volume/36 m ² ; 7.9% of wet is loss on ignition.....	.02
Small gastropods (<i>Thais</i> and <i>Courey</i>)	6 individuals/18 m ² ; .089 gm loss on ignition/individual.....	.03
Animal tissue in corals	19% coverage of coral; .021 gm/cm ² animal tissue in coral.....	40.
Smaller fishes	Visual counts: 25 (21, 23, 24, 25, 34, 34, 17, 33) fish/36 m ² ; 2.42 gms dry/individual and 61% herbivores based on poisoned sample.....	1.0

TABLE 10 (continued).

Biomass Component	Quantity Measured, basis for calculation	Mean Biomass averaged over the Quadrat gm/m ²
Larger fishes	Visual counts: 52 (35, 40, 65, 75, 43)/692 m ² area of horizontal visibility in all directions. 120 gm dry weight/individual; 90% herbivorous; large fishes absent from area 1/3 of time during maximum currents.....	5.0
Total Estimate of Herbivores.....		122.
CARNIVORES PREDOMINATELY		
Mollusca	6 individuals/18 m ² ; .09 gm loss on ignition/individual.....	.03
Small starfish	11 individuals/18 m ² ; 1.0 gm loss on ignition/individual.....	.6
Large starfish	1 individual/36 m ² ; 106 gm loss on ignition/individual.....	3.0
Smaller fishes	39% of fish counted (see herbivorous fishes above).....	.65
Larger fishes	10% of fish counted (see herbivorous fishes above).....	.7
	1 stone fish/36 m ² (100 gm dry) (A stone fish was twice taken from the quadrat area during two days' work)	2.8
Annelids	Estimated 30% of annelids in dead heads (see herbivorous annelids above).....	4.0
Total Estimate of Carnivores.....		11.2

adjunct to visual counts. Many of the larger herbivorous fishes, which abound in coral reefs, travel in active schools and quickly move out of a limited poisoned area. But after the active fishes were censused by repeated counts rotenoning the quadrats revealed the hidden element of small fishes which could then be added to the population estimate.

Herbivorous molluscs, sea urchins, sea cucumbers, brittle stars, and other large invertebrates were counted by hand in subquadrats as the observer carefully took the superstructure of the reef apart, lifting dead material, and breaking open heads with a hammer. The loss on ignition value (600°C) for an average sized organism was used as a rough estimate of live protoplasm to convert numbers of each phyletic type into biomass. Herbivorous molluscs were primarily *Thais*, *Cypraea*, and *Tridacna*.

In the *Herbivorous annelids* were somewhat arbitrarily included all those annelids in sedentary tubes and all those without pharyngeal jaws. These were estimated from sample heads of measured horizontal area coverage carried back to the laboratory and broken open. Allowing the head to stand in stagnant water was found effective in inducing the annelid component to crawl out into the surrounding water prior to death. With estimates of the coverage of

It can be noted that attempting to poison out quadrats or other measured areas with rotenone proved to be a poor census method in itself, but was a valuable

TABLE 11. Dry biomass estimates for quadrat D on the zone of complex large heads.

Biomass Component	Measurement; Basis for Calculation	Mean Biomass averaged over the Quadrat gms/m ²
PRIMARY PRODUCERS		
Algae in live coral	Coverage of live Coral 16% (Fig. 5) .062 gm dry algae/cm ² coral (Table 4)	100.
Algae in shingle (dead coral fragments)	Coverage 10%; .089 gm/cm ² algae in shingle (Table 5)	89.
Algae in tall complex dead heads, encrusting and permeating	Coverage of dead heads; 40%; .049 gm/cm ² algae in and on dead heads	197.
<i>Halimeda</i> clumps in dead heads	Coverage of dead heads 40%; .013 gms loss on ignition <i>Halimeda</i> /cm ² head	52.
Fleshy algae on lower dead parts of tall live heads	Coverage of live heads 16%; 7.5 gms loss on ignition/400 cm ² live head	30.
Algae permeating and encrusting dead cobble under live heads	Coverage of live heads 16%; .028 gm/cm ² algae in sample 25 cm deep in head	45.
Algae in white sand in channels	Coverage of sand 34%; .009 gm/cm ² Algae in sand (Table 5)	31.
Fleshy algae (<i>Codium</i>) on dead-heads along their lateral slopes	Coverage of dead-heads 40%; Estimated fraction of dead-heads with fleshy algae 30%; 36.5 gm dry algae/400 cm ² sample	107.
Algae in <i>Tridacna</i>	Coverage of <i>Tridacna</i> .3%; .040 gm/cm ² dry algae in <i>Tridacna</i>	1.2
Total estimate of primary producers		652.
HERBIVORES PREDOMINATELY		
Sponges in dead-heads	Coverage of dead-heads 40%; 4.0 gm (4, 9, 3, 2) loss on ignition/.04 m ²	40.
Sponges in live heads	Coverage of tall live heads 16%; 7.0 gm loss on ignition/.04 m ²	28.
Midget cucumbers in dead-heads	.27 gm loss on ignition/.04 m ² ; coverage of dead heads 40%	2.7
Small cucumbers in and around heads	2.4 gm loss on ignition/individual; 4 individuals/2.25 m ²	4.3
Small urchins in dead-heads	.13 gm (.19, .06) loss on ignition/.04 m ² ; dead-head coverage 40%	1.3
Ophiuroids and urchins in live heads	.53 gm loss on ignition/.04 m ² ; live-head coverage 16%	2.1
Urchins around heads	27 individuals/2.25 m ² subquadrat; .61 gm loss on ignition/individual	7.3
Ophiuroids around heads	36 individuals/2.25 m ² subquadrat; .40 gm loss on ignition/individual	6.4
Herbivorous annelids in dead-heads	.10 (.09, .11) gm loss on ignition/.04 m ² ; coverage of dead heads 40%	1.0

TABLE 11 (continued).

Biomass	Measurement; Basis for Calculation	Mean Biomass averaged over the Quadrat gms/m ²
Herbivorous annelids in live heads	Coverage of live heads 16%; .14 gm loss on ignition/.04 m ²	.6
Small herbivorous crustacea in dead-heads	Coverage of dead heads 40%; .17 gm/.04 m ² loss on ignition	1.7
Small mollusks in dead heads (herbivores)	Coverage of dead heads 40%; .55 gm loss on ignition/.04 m ²	5.5
Small mollusks in live heads	.09 gm loss on ignition/.04 m ² ; Coverage of live heads 16%	.4
Animal part of corals	Coverage of live coral 16%; .021 gm/cm ² animal tissue in live coral (Table 4) Surface of branching corals about 3 times area covered horizontally	99.
Small herbivorous fishes	Counts on quadrats: 71 individuals/36 m ² ; 2.32 gm dry/individual	4.8
Large herbivorous fishes	Counts per 600 m ² horizontally visible area; 30 (24, 25, 33, 27, 42) fishes; estimated 3/4 herbivorous; 120 gm dry/fish	4.5
<i>Tridacna</i>	.163 gm/cm ² dry	4.9
Total Estimate of Herbivores		126.
CARNIVORES PREDOMINATELY		
Annelids and nemerteans in dead-heads	.07 (.05, .06) gm loss on ignition/.04 m ² ; coverage of dead-heads 40%	.7
Annelids and nemerteans in live heads	.07 gm loss on ignition/.04 m ² ; coverage of live heads 16%	.3
Small crabs and shrimp in live heads	Coverage of live heads 16% 1.05 gm loss on ignition/400 cm ²	4.2
Small crabs around heads	4 individuals/2.25 m ² ; .15 gm loss on ignition/individual	.3
Small crabs in dead-heads	.07 gm loss on ignition/.04 m ² ; coverage of dead-heads 40%	.7
Carnivorous mollusks around heads	5 individuals/2.25 m ² ; .06 gm loss on ignition tissue/individual	.13
Carnivorous mollusks in dead-heads	.5 gm loss on ignition/.04 m ² ; coverage of dead heads 40%	5.0
Small carnivorous fishes	5.3 individuals/36 m ² ; 2.42 gm dry/individual	.34
Larger carnivorous fishes	1/4 of fishes counted in visible horizontal area (See herbivorous fishes above)	1.5
Total estimate of carnivores		13.1

the type of head counted from quadrat maps, these head counts for live and dead head-types were converted into over-all weights per area using loss on ignition values. A correction by counting was made

TABLE 12. Dry biomass estimates on quadrat E—F on the sand-shingle zones of the back reef. (Data combined from open areas of Stations E and F.)

Biomass Component	Measurement; Basis for Calculation	Mean Biomass averaged over the whole Quadrat gm/m ²
PRIMARY PRODUCERS		
Algae in sand	Coverage of Sand 67%; .009 gm/cm ² ; dry algae in sand (Table 5).....	60.
Algae in shingle	Coverage of shingle 33%; .110 gm/cm ² ; dry algae in shingle (Table 5)....	331.
Total estimate of producer biomass.....		391.
HERBIVORES PREDOMINATELY		
Small herbivore fishes	Count 23 (31, 15) individuals/36 m ² quadrat; 2.42 gm dry/average sized fish.....	1.5
Schools of sardine-herring fishes	Count of schools 1.2 (1, 1, 2, 1, 1) per 600 m ² horizontal visible area; About 100 fish/school; 1 gm/fish.....	.2
Large herbivore fishes	Count 16 (16, 14, 17, 15) individuals per 600 m ² horizontal visible area; 240 gm dry weight per fish.....	6.4
Total estimate of herbivores.....		8.1
CARNIVORES PREDOMINATELY		
Larger fishes other than sharks	3.2 (4, 0, 6, 3) individuals counted per 600 m ² horizontal visible area; 240 gm dry weight/fish.....	1.3
Sharks observed while walking across back reef zones	Counts per 20 minutes observation: 1.6 (1, 1, 0, 5, 1) individuals per 600 m ² visible area; 90 degrees visibility at one time; each individual in sight about 30 seconds; Weight per shark about 50 lbs wet or 4540 gm dry (20% of wet) (Vinogradov 1953).....	prorated on time and area basis 1.2
Total estimate of Carnivores.....		2.5
DECOMPOSERS		
Foraminifera	Counts: 54/cm ² area 1.33 x 10 ⁴ gm loss on ignition/individual (13.5%) 67% coverage	48.

for tube worms imbedded in the hard base reef of the front quadrats.

Small *Herbivorous crustacea*, including mainly shrimps and gammarids, were estimated in the same manner as herbivorous annelids.

Micro-crustacea in the algal encrusting mats were estimated from some counts in samples scraped from measured areas. Only 237 (361, 120, 180, 288) were found per 28 cm². Estimating .02 cm x .01 cm x .01 cm as the size of these small species and allowing 14% dry tissue in wet volume (Vinogradov 1953), a negligible biomass of .022 gms/m² is found.

CARNIVORES (OTHER THAN CORALS)

Small *carnivorous fishes*, including mainly wrasses, groupers, and small moray eels, were estimated by

means of counts and rotenone as described for herbivorous fishes. *Gymnothorax buroensis*, *Thalassoma quinquevittata*, *Epinephalus hexagonatus*, *E. spilotoceps*, *E. merra*, *Amblycirrhitus arcatus*, *Scorpaena parvipinnis*, and *S. gibbosa* were examples of fishes in this ecological group.

Large *carnivorous fishes*, including a variety of species with no one type predominating, were very roughly estimated by counts as with the herbivorous fishes. A rough estimate of shark biomass was obtained as follows: The time sharks were in view during the 15 minute underwater walk to and from the area across the back reef zone was recorded. The fraction of the time when a shark was observed was assumed to be the fraction of one shark's range in view. The area of visibility of an observer looking from side to side through a face mask was assumed as 1/4 of 360 deg. The average shark had an estimated weight of about 50 lbs. wet. Moray eels were estimated from the rotenone samples on the surely underestimating assumption that all the morays had climbed out into the channels to die. A rough estimate of area effectively rotenoned was used.

Carnivorous annelids including mainly the nereids were estimated as described for herbivorous annelids.

Carnivorous crustacea including mainly small crabs were estimated as described for herbivorous crustacea.

Carnivorous molluscs primarily *Conus* were estimated as described for herbivorous molluscs.

One series of night counts was made to estimate the larger night invertebrates. The basis for estimation was the number seen in walking a known distance where estimated visibility for bright eye reflections with an underwater flashlight is about 2 ft as a band along the path. A count of 6 individuals (4 spiny lobsters, 2 large crabs)/720m² was obtained. One individual weighed 150 gm wet with about 35 gms organic matter as estimated by loss on ignition. Thus about .3 gms/m² was observed.

DECOMPOSERS

Decomposers are here identified as that trophic group that subsists on the leakage from other food chains of dead organic matter no longer clearly assignable to a living group of producers, herbivores or carnivores. Included in this group are the bacteria, blennies, and foraminifera. Many others act as decomposers in part of their diet in nature, as when sea cucumbers eat sand, but in most of these cases a majority of the nutrition is from living algae. All algae are considered producers even though some may erode calcareous skeletons. The following were the only efforts made to assess the decomposer part of the community.

Bacteria. Counts of bacteria on glass slides suspended three weeks indicated an 80% coverage. What proportion of these were autotrophs of photosynthetic or chemosynthetic type is not known. As a possible upper limit, the surfaces of all reef objects (about 3 times horizontal area in complex zones) may be assumed to be bacterial covered to the same extent.

Allowing .05 gm/cm³ dry weight and a one micron thickness of bacteria an estimate of their possible biomass of .1 gm/m² results. We have no idea of the bacterial populations within skeletons.

Foraminifera. The foraminifera of the front reef algal mats are very small forms (.1 mm) characteristic of plankton and probably maintained by influx of oceanic water in the strong flow in this area. The forams of the sandy back reef are large benthic types like *Calcarina* (1. mm). Rough counts (Table 7) and loss on ignition values for these components permit rough estimate of their contribution to the biomass. The nutritive source for the large foram biomass (Table 12) on the back reef is not known.

Blennies. Following food studies by Strasburg (1953), the blennies which are numerous in rotenone samples from the algal ridge zone can be grouped as partly decomposers because of their eating of precipitated detritus (leptopel).

These exploratory estimates were mainly incidental to our study. An understanding of the trophic relationships of the bacteria and foraminifera on reefs is urgently needed. From estimates available, these components do not represent a large biomass in comparison to the other trophic levels. However the high metabolic rates of the small decomposers life system greatly magnifies the effect of a small biomass.

BIOMASS PYRAMIDS

Finally, the quantitative trophic structure of the reef community can be set out as a pyramid of mass. The estimates of biomass by trophic level as estimated in the previous sections are combined in the graphs of Figure 10. In spite of the various errors in the necessarily crude estimates, a general pyramid structure clearly results in all cases as predicted by ecological theory. Furthermore, these pyramids are not quantitatively too different on a weight basis from quadrat to quadrat even though entirely different types of reef community components are represented. Thus the combined mean estimates in the composite pyramid (Fig. 10) gives a reasonable picture of relationships of standing crops. Even if any one of the minor estimates were as much as two fold in error, the general shape of the pyramids would be unchanged. If the chlorophyll to organic matter ratio (Fig. 8) has been underestimated by using Codium, the correct pyramids may be steeper than shown in Figure 10. The ratios of standing crop between trophic levels is H/P 18.9%; C/H 8.3%. Decomposer estimates do not include all components and are left out of the pyramids. Although the reef in gross appearance is what is usually described as a coral reef (rather than an algal reef), and although even the front breaker ridge is in gross appearance half coral, the pyramids show that on a live protoplasmic basis the usual predominance of producer algae exists. This is partly due to the prevalence of plant protoplasm in coral and partly due to large concentrations of matted algae in and on all the reef surfaces.

The pyramids of biomass structures show up even

within some taxonomic groups. In the fishes, for example, there is a striking predominance on a weight basis of herbivorous parrot fishes, surgeons, damselfishes and butterfly fishes in comparison to wrasses, groupers and other carnivores. The numerous, beautiful schools of brilliant herbivorous fishes are indeed the "cows" of the reef.

The single coral is first a producer, to a lesser extent (in many cases) an herbivore, and somewhat a carnivore, thus giving something of a pyramid within one coral head. Indeed the isolated coral heads growing in Eniwetok atoll lagoon practically constitute a whole community since the plankton is scarce and so much of the metabolism is internally complete, thus fitting community definition. This need not be true of all coral heads everywhere and is most certainly not the case for clusters of non-photosynthetic *Dendrophyllia* growing in deeper waters at Bikini or in shadows of ledges in Hawaii.

COMMUNITY METABOLISM

Having demonstrated roughly the trophic structure of the coral reef, consideration may be given the rates at which the community is operating, its productivity, its metabolism, its turnover, and the efficiency of its primary production. Although there is consensus that individual corals are not quite inherently self sufficient in production, the work of Sargent & Austin (1949, 1954) suggests that the whole reef does subsist on its own primary production. They showed, using black bottles, that the production values of water in both the open sea and lagoon side of the reef were far too small to be of significance in comparison to the production of the whole reef, although this did not prove that plankton passing over the reef was not quantitatively an important source of nutrition. Their production measurements only meant that production by the plankton while passing over the reef was small relative to the attached community below. Whether the large volume of water filtered by the reef was contributing appreciable energy sources from organic matter previously accumulated in the water was not settled. Whether the reef lives entirely on its own production or not, it is likely that it derives critical nutrients from the strong flow over the community.

In this study, to assess the contribution of the inflowing water to the reef metabolism, measurements of several variables were made in incoming sea water (represented by water in the windward channel south of Japtan island), in water crossing the front reef after passing through the breaker zone, and in water leaving the reef over the back reef zone (Table 13). The general water characteristics are summarized in Table 14. Discussion follows on the significance of the changes observed as indicated in Figure 11.

Sargent & Austin (1949) interpreted their high values of organic matter on the front reef as due to the trajectory of the water in passing through several turbulent eddies in the breaker zone at which time some of the production of the buttress zone was con-

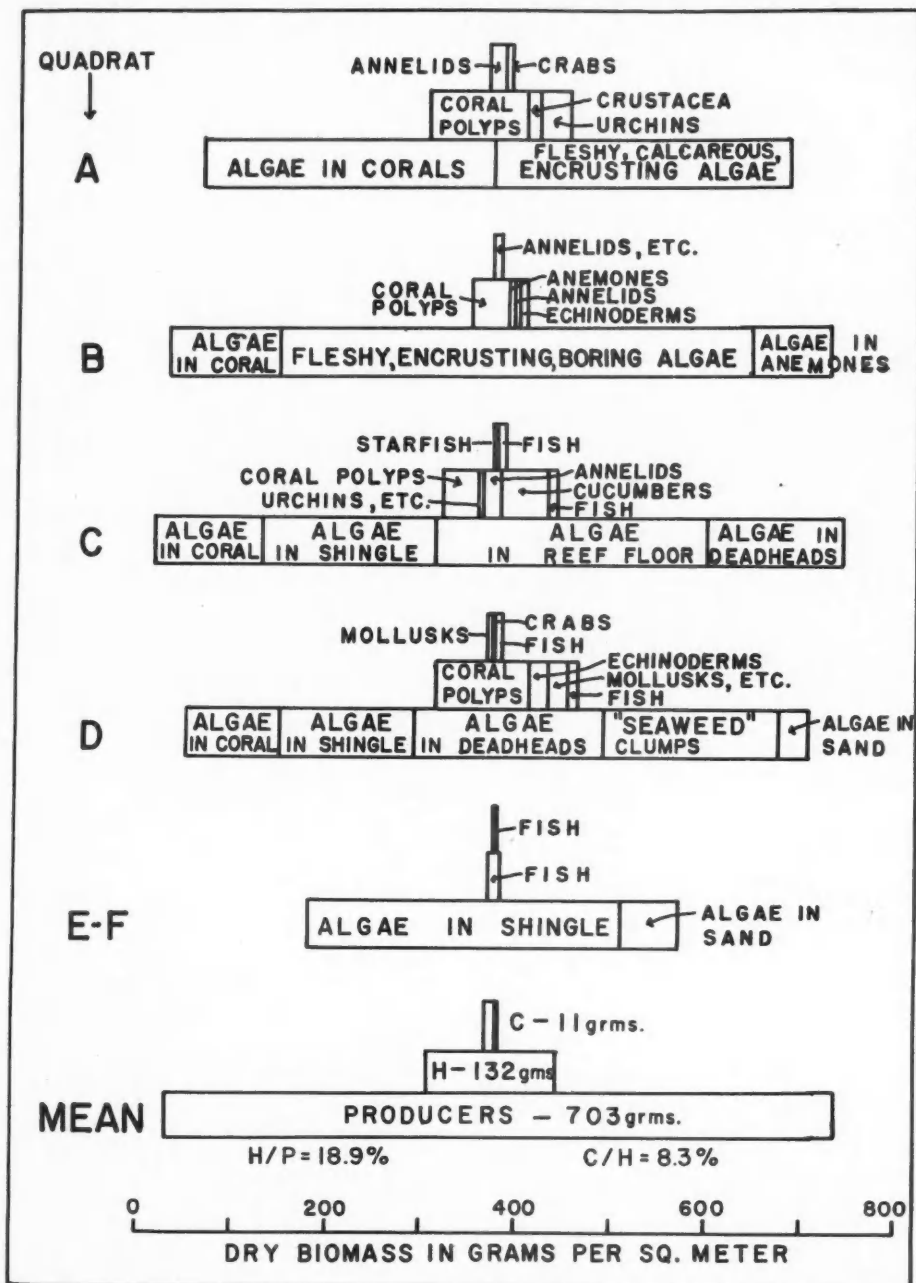


FIGURE 10. Pyramids of biomass resulting from estimates of the dry weight of living materials (excluding, of course, dead skeletal materials associated with protoplasm). For each quadrat, A-F, the weight of "producers" (bottom layer of pyramid), the "herbivores" (H) (middle layer), and the "carnivores" (C) (top layer) is shown, and also the average dry biomass for the reef.

TABLE 13. Plankton characteristics across the reef, July 1954.

Station, circumstance	Volume Filtered m ³	Dry Weight gm/m ³	Loss on ignition gm/m ³	Washed ash (dry) gm/m ³	Plant Fraction (Extract method) %	Radioactivity Thds. counts min/m ³
OCEANIC WATER (taken from M boat in Japtan—Parry channel)						
10:30 p.m. (night), July 19, falling spring tide:						
Sample 1	6.1	.0120	.0041	5.5%
Sample 2	6.1	.0121	.0042	.0059	13.5
2:00 p.m. July 17, rising spring tide:						
Sample 1	6.1	.0177	.0064	6.5%
Sample 2	6.1	.0099	.0036	.0054	24.1
Mean Oceanic Water0129	.00457	.0057	6.0%	18.8
WATER CROSSING ALGAL-CORAL RIDGE						
Midnight, July 19, turning low spring tide	3.6	.057	.030	.023	41.2%	188.
2:10 a.m. (night), July 19, rising spring tide	5.0	.063	.033	29.7%
Noon, July 17, turning low spring tide	4.4	.358	.175	.181	28.7%	1081.
10:45 a.m. July 27, falling spring tide	9.0	.039	.021	.0168	57.2%	73.
Mean of water crossing algal ridge129	.064	.074	39.2%	447.
WATER CROSSING END OF ENCRUSTING ZONE (Station B-2)						
4:00 p.m., July 13, falling neap tide	21.8	.079	.022	.0236	8.1%
WATER CROSSING ZONE OF LARGE HEADS (Station D)						
July 13, turning high neap tide:						
Sample 1, 3:00 p.m.	30.0	.024	.0079	.0034	32.3%
Sample 2, 3:20 p.m.	30.0	.027	.0099	.0054	30.6%
July 19, rising spring tide, Night:						
Sample 1, 1:00 a.m.	1.68	.054	.0327	3.3%
Sample 2, 1:37 a.m.	2.65	.034	.0199	.0081	52.
July 17, turning low spring tide:						
Sample 1, 10:53 a.m.	11.9	.0129	.0052	20.7%
Sample 2, 12:40 a.m.	5.9	.035	.0139	.0171	77.
July 27, falling spring tide:						
9:45 a.m.	3.0	.037	.0184	.0125	34.
Mean of water crossing large head zone032	.0154	.0093	22.0%	54.
WATER CROSSING ZONE OF SAND AND SHINGLE OF THE BACK REEF SHELF (Station E)						
July 27, falling spring tide, 8:50 a.m.	4.0	.022	.0119	.0042	35.

tinually being added. The plankton data suggests this picture to be correct for coarse plankton. Organic matter data are inconclusive as to whether the far larger dissolved organic-matter fraction changes in crossing the reef.

As the water passes the shallow portions of the reef, much plankton is removed. That which remains is exposed to settling in the quieter back waters and to the schools of small anchovy type fish of the back reef zone. The presence of some open-sea plankters in the samples of the back reef indicate that a few individuals do cross the reef without being removed. In general the reef is a highly efficient filter even though the water crosses the reef in 15 to 20 minutes.

Because the tidal cycle creates a variation in the current the reef plankton is highly variable. At very low tides the breakers up front pull off usual quanti-

ties of algae but since little water is being thrown up and over the reef, they accumulate in the breaker eddies until the incoming tide at which time the plankton is unusually heavy in the water first coming over the reef. Some such variation may account for the organic values of Sargent & Austin (1949) which were too high on the front reef relative to the back reef to match the known respiration of the reef. The high plankton values in Sample 1, 2:00 p.m. July 17 (Table 13) are due to the effect described above. The data in Figure 11 show similar patterns across the reef for loss on ignition, chlorophyll extracts of the plankton, and plankton radioactivity.

FLUX OF LARGER PLANKTON

Plankton samples were made with a #10 net. On the reef the net could be set on a stake to permit the

TABLE 14. Chemical levels in Eniwetok waters.

Component	Analyses	Mean	Range
Organic Matter, alkaline permanganate method, in mg/l.	13	.96	.74-1.41
Nitrate nitrogen, strychnidine method, in mg atoms/m ³	24	.44	.06-1.0
Inorganic phosphorus, ammonium molybdate method in mg atoms/m ³	29	.32	.26-.64
Total phosphorus, acid digested, in mg atoms/m ³	6	1.7	0-3.4
Dissolved oxygen, Winkler method, in mg/l.			
(1) Incoming Ocean Water (from channel)	8	6.54	6.38-6.68
(2) Algal-coral Ridge	12	6.50	6.09-6.97
(3) Back Reef zone of Large Heads			
Daytime	19	7.31	6.22-8.59
Night	6	5.37	4.89-6.26
pH (Beckman Model G)			
Daytime			
Incoming Ocean Water (from channel)	5	8.21	8.19-8.22
Algal-coral ridge	5	8.21	8.18-8.24
Back Reef zone of large heads	5	8.32	8.30-8.33
Night			
Incoming Ocean Water (from channel)	2	8.19	8.18-8.19
Algal-coral ridge	2	8.16	8.14-8.17
Back Reef Zone of large heads	2	8.10	8.10-8.10
Temperature in degrees Fahrenheit			
Incoming ocean water (from channel)	2	82.6	82.6-82.7
Algal-coral ridge	2	82.9	82.7-83.0
Back reef zone of large heads			
Daytime	3	84.1	83.5-84.6
Nighttime	1	82.2

strong current to flow through. The channel samples were taken from a boat. The volume of water passing through the net was determined by placing a drop of dye (air-sea-rescue dye marker, fluorescein) in the mouth of the net and counting the seconds required for the dye to wash through the net. The current on the reef was always sufficient to give a satisfactory sample of plankton after 10 to 40 minutes. The current outside the net was simultaneously determined with the dye method in order that computations of total plankton flux could be made. The average time for five dye spots to cross a distance of 20 ft was used to determine water velocity.

Qualitatively, net plankton of the incoming water was characterized by pteropods, calanoid copepods, radiolaria, and tiny filamentous algae. The reef plankton after passing the surf zone was conspicuously different being made up of large fragments of filamentous algae derived from the buttress-breaker zone of the reef. The data (Table 13, Fig. 11) clearly indicate a very large increase of large-sized plankton as the water crosses the breaker zone and a rapid loss of most of this plankton in crossing the rest of the reef. Thus the reef consumes its own pseudoplankton. Since the amount of plankton leaving the reef at the back is about the same or slightly greater than that in the incoming water, it seems that the reef is indeed energetically self-sustaining and deriving no net gain of larger planktonic material from the inflowing water. The data, however, do not entirely eliminate the possibility of a gain from nannoplankton and dissolved organic matter.

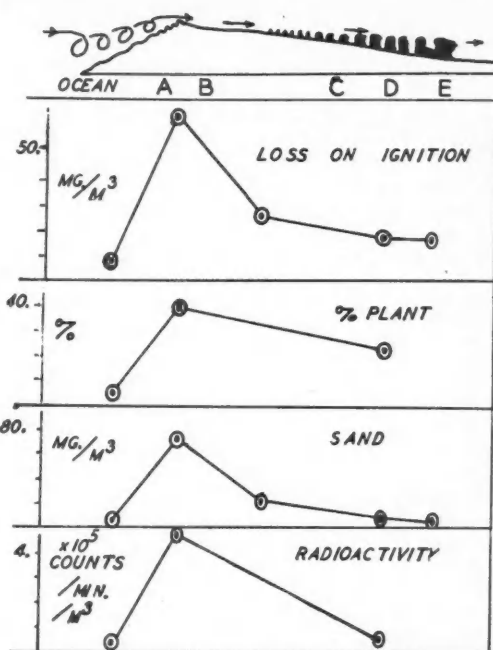


Fig. 11. Changes in water content as it crosses the reef in regard to: loss on ignition of net plankton and seston; green plant content (estimated by chlorophyll content) of net plankton; suspended sand; radioactivity.

TOTAL ORGANIC MATTER

A few measurements to determine the order of magnitude of the total organic matter were made with the alkaline permanganate method of Benson & Hicks (1931). Samples (100 cc) were digested 30 minutes at 95°C with standardized permanganate and sodium hydroxide. The ferrous sulfate was added in an amount equivalent to the permanganate. Oxidation-reduction conditions were adjusted with manganous salts and phosphoric acid to prevent oxidation of the chloride. The excess ferrous sulfate was titrated with more permanganate to determine the permanganate lost during digestion. A mean value of about 1 mg/l of oxygen consumed was found (Table 14). The values obtained with this very rough procedure were fairly consistent and probably give the general order of magnitude of dissolved organic matter. Significantly, the values were similar to those obtained by Johnstone with BOD determinations (Sargent & Austin 1949). We did not find the great difference between front and back reef found by Sargent & Austin although our permanganate method should probably not be relied upon as accurate enough to delimit a difference of less than 1 ppm. As in other kinds of water, the dissolved organic matter is much greater, though less conspicuous, than the particulate matter. Motoda (1938) found 2.0-3.1 mg/l, 35 day BOD, in open sea water at Palao and 5.5 mg/l in the bay.

PRODUCTION AND RESPIRATION BY
THE FLOW METHOD

Sargent & Austin (1949) used an ingenious flow-rate method to measure the over-all production and respiration of the coral reef at Rongelap Atoll, Marshall Islands. A similar method has been used by H. T. Odum in Silver Springs, Florida (1953, 1954). The oxygen content of the water upstream and downstream is measured simultaneously. The oxygen increase between stations during the day is the net photosynthetic production of the community. The oxygen decrease between stations during the night is the total respiration of the community. By taking a series of measurements over the daily cycle, one obtains the course of production during the day. Measurement of the current transport permits calculation of total reef metabolism. The respiration at night plus the net production during the day gives the total production. By comparing the area of the graph between the day curve and the zero line with areas of the graph under the zero line at night one can obtain an indication of what part of the excess production during the day is used up by respiration during the night.

A series of such measurements was made on several different days of typical cloud cover of from 1/10 to 3/10 small cumulus and 1/10 to 4/10 high and middle cloudiness, and also at night. These values are expressed on an area basis in Figure 12 following their conversion from depth and current measurements. The curve obtained by Sargent and Austin for their reef is also plotted in Figure 12.

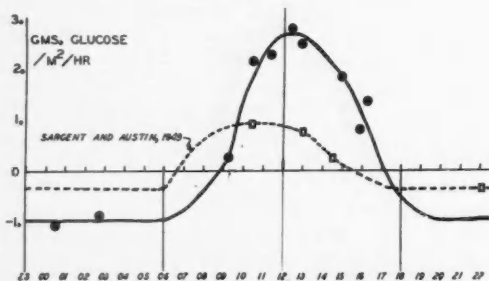


FIG. 12. Graph of primary production and respiration on the middle reef between the coral-algal ridge and quadrat D. A similar curve from Rongelap Atoll is recalculated from Sargent & Austin (1949).

Besides small errors due to inherent fluctuations and variability of oxygen samples and methods, current and depth measurements, and cloud cover changes, there is a major source of error that tends to cause values of production and respiration to be too small. This is the diffusion of oxygen from and to the atmosphere. This error is greatest when the displacement of the gaseous content of the water from equilibrium with the atmosphere is greatest. Thus the error in decreasing the production estimate is greater than that in the respiration since greater displacement from equilibrium occurs. Furthermore, during the day's production a carpet of bubbles of

oxygen is observed to form over the algal-mat surfaces particularly on the front reef. These bubbles are continually breaking off and reach the surface without dissolving so that some of the oxygen is lost, further lowering the estimate of production below the correct figure. The diffusion error is further discussed in the section on over-all balance sheet for the reef.

Our curve of reef production for the middle reef (Fig. 12) permits the following interpretations: (1) The productivity of the reef is very high, greater than 24 gms/m²/day or 74,300 lbs/Acre/yr. (2) The productivity is greater than that of Silver Springs, Florida, which is very nutrient-rich with a relatively constant temperature, and supports a similarly autotrophic community with a production of 50,000 lbs/Acre/yr (Odum, H. T. 1953-54). Silver Springs has a higher summer production rate but a smaller annual total due to the small insolation of the winter. The reef production is greater than other marine localities reported. In comparison to the open tropical waters such as that flowing onto the reef (.2 gms/m²/day; Sargent & Austin 1949), this reef is 120 times more productive. (3) The Japant reef has twice the production value per area by the flow method as the Rongelap reef studied by Sargent & Austin. The larger production of the reef per area is matched by a larger respiration per area in comparison to the reef studied by Sargent & Austin and therefore suggests a greater biomass per area. Sargent & Austin (1954) describe their reef as relatively barren. (4) There is a lag between the sun's light intensity and the oxygen production as measured in the water above the reef each day. It is likely that part of this lag is due to the location of many of the primary producers down in the calcareous reef surface, sands, and below the coral polyps.

In view of the evidence for a lag in gaseous exchange, a symmetrical morning and afternoon production curve seems incorrect even though Yonge & Nicholls (1931) showed that isolated single corals in the sun may reach maximum photosynthesis in the morning. Thus Sargent & Austin's production curve, drawn through three afternoon points, probably shows too much productive area. It seems likely that their reef possessed little or no excess of production over respiration and may not have been depositing stored organic biomass.

PRODUCTION EXPERIMENTS IN SUBMERGED BELL
JARS AND PLASTIC BAGS

Following experience in Silver Springs, efforts were made to enclose reef components with glass jars, and to sample the water before and after periods of production and respiration. After many difficulties a diaphragm of inner-tube rubber placed outside of the glass jar was found to make a seal between the jar and the hard irregular reef floor. Sand and boulders heaped over the ring-shaped rubber border prevented active circulation of the water outside the jar with the interior water. A rubber tube with an

opening inside the jar and one outside the jar permitted sampling. Water samples were drawn out with a type of sampler developed at Silver Springs by which the observer draws water through two bottles on a stick by sucking on a tube. The bottle nearest the bell jar source is used for Winkler oxygen determinations after the second bottle has filled.

The unexpected results given in Table 15 for experiments on the reef seem to demonstrate a lag effect as also evidenced in the flow measurements discussed in the previous section. When black covers were put over corals or reef surfaces during the day, oxygen, presumably from sub-surface bubbles, continued to be evolved for over an hour. Supporting this interpretation is the observation that myriads of little bubbles rise from the interior of *Millepora* or *Acropora* fingers when they are broken during the day. The hard bumps of the reef surface that do not even look green externally, as well as the algal mats of the front reef, are coated with bubbles during the middle of the day. These bubbles on bare looking places are probably coming from the subcrustal green algal layers previously described in the primary producer discussion.

To determine whether reef components had an over-all net production or respiration, plastic bag experiments were conducted in the field. Following the suggestion of Dr. Max Doty, 6 x 6 in. plastic bags were tied around small coral and algal heads with rubber bands and observed a day later. The bubbles which accumulated in the bags are assumed to have been initially formed of oxygen because release of other gases seems unlikely. Carbon-dioxide would not be released in a gaseous form through basic sea water. Since no temperature changes could occur in this field arrangement, air components would not be released from solution. Once a gaseous phase was formed other dissolved gases might enter. No extensive decay is suspected that might produce large quantities of hydrogen, methane or other gas. As positive evidence that these bubbles contain considerable oxygen, water drawn from bags with bubbles was super-saturated whereas water drawn from bags without bubbles was undersaturated. However, after a gaseous phase had been formed, other dissolved gases would diffuse in. Visual estimates were made of the volume of bubbles in the bags after one day. Note (Table 16), that the dead heads with encrusting algae have a large net bubble-production whereas the corals had slight or no production even though 2 hrs

TABLE 15. Lag in gas exchange between reef and water. (Oxygen changes in dark and light bell jars on reef substrates.)

Surface	Preceding Light Regime	During Measurements	Time Lapse Minutes	Oxygen Change gms/m ² /hr
Sand-shingle.	7 hr light	dark	31	+ .73
Sand-shingle.	31 min dark	light	30	- .24
Dead-heads..	7 hr light	dark	31	+ .085
Dead-heads..	3 hr light	dark	73	+ .125

TABLE 16. Volume of bubbles accumulating in plastic bags over reef heads. Bubbles estimated at noon.

	Time exposed hrs	Volume of bubbles cc
Dead heads permeated and encrusted with algae.....	26	15
	74	12
	26	25
<i>Halimeda</i> bunch.....	26	2
Bag of foraminiferal sand.....	26	.1
Live corals		
<i>Millepora</i>	26	.5
<i>Porites</i>	26	1.0
<i>Heliopora</i>	26	1.0
<i>Acropora</i> (read at 9:00 a.m.).....	70	0
<i>Acropora</i>	50	.1
soft coral (<i>Lobophytum</i>).....	26	.1
Control bag.....	26	.1

of sunlight of a second day were included in more than one day's measurement. This seems to indicate that photosynthesis in situ does not exceed respiration in many corals although it does match a large fraction of the respiration. It is possible that the role of photosynthesis is greater in the clear waters of the Marshalls than in more turbid waters in some other areas. Perhaps fortunately for corals, decreasing light, due to greater turbidity is often accompanied by increasing plankton content.

PHOSPHORUS AND NITROGEN

To establish the general nutrient level on the reef, a few analyses were made of inorganic phosphorus, organic phosphorus, and nitrate nitrogen. Methods used were rough adaptations of the ammonium molybdate-stannous chloride method for phosphorus (Robinson & Kemmerer 1930) and the strychnidine method for nitrate (Zwicker & Robinson 1944). Samples were necessarily determined 1 to 6 hrs after collection. Some loss due to uptake by bottle walls may have occurred. As expected for a central tropical ocean the incoming waters had extremely low values of both nutrient elements. Although the concentrations were in the lower limits of sensitivity of the methods, the values reported in Table 14 possibly are of valid order of magnitude.

Considering the productivity, as established, the required nutrients can be accounted for as follows. If the mean nitrogen content of the producing algae is 3.0% ($\frac{1}{2}$ protein), then .72 gms/m²/day nitrogen is required. Considering the width (Table 17) and volume transport of water (3×10^4 m³/day), only .6 gms/m²/day nitrogen could be supplied from inorganic nitrate even if it were all captured and used. It is not all used since it was detected in a concentration of the same order of magnitude in back-reef water. Using open-ocean values (Sverdrup, *et al.* 1946) .1 gm/m³ total organic nitrogen is found in water with about 2.0 gms/m³ total organic matter. Using this nitrogen/organic matter ratio of 5% and a total organic matter content of 1 gm/m³ (as determined, Table 14), about 4.7 gms/m²/day could be

TABLE 17. Balance sheet for the Japtan inter-island reef in July. From algal-coral ridge to the end of the zone of large heads, this zone is 322 m² long.

	gm/m ² /day
INCOME*	
Planktonic organic matter (Table 13) from breaker zone.....	2.0 [‡]
Primary production (measured as oxygen, calculated as glucose:	
Net (uncorrected) daytime production.....	14.0
Respiration during daytime.....	10.0
Total income.....	26.0
LOSSES*	
Planktonic organic matter lost to lagoon (Table 13).....	0.4 [‡]
Total respiration in 24 hr.....	24.0
Total outgo.....	24.4

*Dissolved Organic Matter; 0.96 gm/m³ (Table 14) (no significant difference between influx and outflux; analytical method not precise enough, however, to delimit.)

[‡]The mean water flux during plankton sampling was 425m³/hr across a band of reef 1 m wide.

acquired by the reef if all the nitrogenous organic matter were taken up. To meet the need of .72 gms/m²/day, therefore, much of the incoming organic matter would have to be taken out. Our few analyses showed no evidence of this magnitude of organic-matter uptake although Sargent & Austin had some evidence of large uptake. It seems equally likely that there is cyclic re-use of nitrogen along with some nitrogen fixation by the abundant blue greens of the front reef. That the surface encrusting algae are so definitely correlated with high current velocity, however, suggests the need for taking out some nutrients of organic or inorganic nature from the low nutrient water. As indicated in Table 5, however, the surface encrusting algae, although conspicuous, are relatively unimportant on a biomass basis in comparison to the algae permeating the calcareous substrates, living and dead. They may, however, have higher metabolic rates than the imbedded algae.

Similar calculations suggest that phosphorus is more abundant relative to needs than nitrogen.

The back reef production is accomplished largely by algae within the calcareous dead parts of corals and other back-reef components. The coverage of coral decreases from nearly 50% of the front reef to 16% of the back reef and finally 0%. Apparently, nutrients caught and stored by the algae and coral of the front reef are passed to the back-reef producers in the form of skeletal fragments. The front reef encrusting-producers, being in shallower water with much swifter currents (Fig. 2), are exposed to greater volume per individual so that the energy of nutrient gathering is partly supplied by the flow system. Thus an adequate nutrient source in water and plankton is available at the front. The nutrient and current regimes are thus entirely different for the front and back-reef producers. The front-reef producers need catch only enough nutrients to balance

that leaking off the back reef to maintain the ecosystem. The general habit of the boring producers in all the reef surfaces is most favorable to nutrient conservation. One imagines that at the time of a typhoon or other circumstance bringing richer water to the surface of the ocean, the reef would capture critical nutrients in an efficient manner for future use. Certainly the reef has concentrated radioactivity of multiple types in water that is barely above background as it drifts in 200 mi. from Bikini. Three samples of water, evaporated down without filtering, gave mean radioactivity of 182 counts/min/l (determined by K. Lohman). This was roughly of the same magnitude as the dried-plankton radioactivities per volume (Table 13) estimated with a Beta Gamma survey meter (AEC MOD-SGM-2B). Coral and algal surfaces registered about 300 counts/min/cm² of surface. Thus, plankton radioactivity of a liter of water has an order of magnitude equivalent to that of a cm² of coral surface.

The reef surfaces, living coral, living calcareous algae, and dead skeletons all act as a kind of soil in that they conserve phosphorus nutrients and permit plant biota to burrow in to reach these nutrients. As indicated in Vinogradov (1953), fresh coral skeletons have 1% phosphorus and .01 to .1% aluminum and iron. Calcareous algae contain much less. Green layers of boring algae are found just under the red surfaces of calcareous red algae as well as under the corals (Fig. 7D).

The N/P ratio by atoms is roughly 2.1 (using a nitrogen value inferred from organic matter on the assumption that most is protein), which indicates particularly sparse nitrogen conditions. The large proportion of small blue green algae may suggest a low nitrogen environment.

REEF DEPOSITION, REEF EROSION, pH CHANGES

Although the production and respiration measurements suggest that respiration is not far from a balance with production, there is little clear evidence about the balance between skeletal reef deposition and erosion of any one reef yet studied. Certainly the reef atoll as a whole can maintain its relationship to sea level for long periods of time. As carefully postulated by Mayor (1924), a reef seems to have the mechanism for self regulating its balance of deposition and erosion at about 6 in. below mean low water spring tide. The excess of production or respiration does not in itself indicate whether deposition or erosion is in excess. For example, animals like oysters with entirely respiratory metabolism may nevertheless relegate energy to deposition. Most marine plants with a primarily production-type metabolism do not deposit a skeleton which their metabolism would tend to precipitate in water almost saturated with respect to calcium carbonate, like that at Eniwetok. This might involve an energy expenditure. It is not clear whether reefs, by a succession, destroy themselves by becoming a terrestrial community or whether they form a climax at the 6 in. level below low water spring tide.

Sargent & Austin attempted to estimate reef deposition on the assumption that most of the reef biomass was coral and that their respiration measurements for the whole reef would be extrapolated into a deposition rate, assuming a deposition to respiration ratio typical of corals as measured by previous workers. However, it is clear from the pyramids (Fig. 10) that the majority of the biomass is not coral-animal tissue.

Nor is the metabolism predominately coral. By calculation from Mayor's value for metabolism per living biomass of .43 mg/gm/hr (mean of 4 species) and our figure of .062 gms/cm² total biomass in corals, and a coverage of 20% coral, one obtains a respiratory contribution of coral of 53 mg/m²/hr. This is a relatively small part of the total respiration of the reef determined with the flow method which is about 1.0 gm/m²/hr.

Sargent & Austin's possible overestimation is partly counteracted by the use of the wrong density. Even so, their over-all estimate of maximum material added (1.4 cm) seems too high, on the basis of their calculations.

As a variation of Mayor's calculation the quadrat estimates of coral coverage were used to estimate rate of coral deposition with a figure for coral growth derived from Mayor (1924). Slightly lower growth rates are found in colder waters (Tamura & Hada 1932, Ying 1934). By recalculating on an area basis and averaging 18 growth values for corals from Mayor, an annual skeletal growth rate of 8.0 cm was obtained. This involved using a dry gross density of coral of 1.9^g gm/cc. Most of our reef seems to be built of coral (not calcareous algae) if one can judge by blocks of the reef from the dynamite holes elsewhere on the atoll (Parry island) or from the present composition of most of the reef. Much of the deposition, therefore, comes from the 20% coverage of coral. Therefore, the 8 cm skeletal growth in the areas of coral is spread over the whole area in the form of shingle and dead heads to form a net addition of material of growth of 1.6 cm. Although this rate of increment is almost identical with the one estimated by Sargent & Austin, their apparently less productive reef may actually have a lesser depositional rate.

On the basis of growth rate and coverage estimates, and a density of 1.8, Mayor estimated 0.8 cm annual deposition and simultaneous erosion on his study reef in Samoa.

For the middle reef the estimate of 1.6 cm calcareous deposition amounts to 3.05 gm/cm²/yr. The over-all income of 26.0 gm/m²/day (Table 17) is

* In Table 3 are given density measurements of two types. One is the density of the dried skeletal material obtained by weighing wet while suspended in water and by weighing dry. This density which is of interest mineralogically is the weight per volume of the component skeletal septa. The density of a dry gross block including the empty pore spaces is considerably less and is obtained by correcting for pore space. Although the skeletal density (mostly aragonite) is about 2.3 gm/cc (Table 3), with a pore space of 16% the dry blocks of coral have a gross density of only 1.9 gm/cc. This latter density should have been used by Sargent & Austin rather than 2.5 gm/cc in estimating growth increment from weight increases. This error fortunately partly counteracted their error of overestimation of coral populations discussed above. When the pore space is filled with water, the gross wet density is 2.1 gm/cc, a sometimes useful quantity.

equivalent to .95 gms/cm²/yr glucose. Thus the biomass initially deposited is only 1/3 of the calcareous deposition. With the water near the inorganic deposition point, little energy is likely to be required for this calcareous deposition. Just how much is not yet known.

This coral increment being added is very likely being eroded just as fast by current abrasion and the complex of bacteria and boring algae that characterize the coral shingle fragments that dominate much of the back reef zones, so neither the above calculation nor Sargent & Austin's evidence is at all indicative of over-all net reef growth or erosion.

Some idea of the magnitude of abrasion taking place on the front buttress zone, which must be balanced by growth to maintain the reef and must be exceeded to produce a reef-growth laterally into the wind, may be obtained from the sand in the reef plankton. The plankton ash in the samples collected at the front and back reef was washed with water leaving a residue consisting mainly of fine calcium carbonate sand that had been suspended in the water passing through the plankton net. The change in this sand fraction in crossing the reef is depicted in Figure 11. Strikingly, the sand content rises in crossing the breaker zone and as the current diminishes on the back reef the sand content falls, thus demonstrating the action of front-reef growth in filling in and cementing the back reef. Since no measurements of sand in plankton were made during the strong currents of high tide, the magnitude of deposition and erosion of reef sand is uncertain.

BALANCE SHEET FOR THE REEF COMMUNITY

Having made various measurements and estimates of photosynthetic rates and metabolic processes, we may now consider the data as a whole to see how nearly balanced are the gains and losses of organic matter on one reef section. In Table 17 the sources of energy storage gain are estimated, including primary photosynthetic production and influx of organic matter in the water. The losses of energy are also listed, including respiration, and outflow of organic matter. The gains and losses are only 4% apart. In view of the rough nature of some of the estimates it is not certain whether this is a significant difference or whether the community is in a perfect steady state with losses matching gains. With the 15-20% lower total insolation in winter (insolation tables, Kennedy 1949) at this latitude than when these measurements were made in July, a lower production but relatively unchanged respiration may be expected to make an annual balance between production and respiration.

This vigorously productive reef is possibly one of those that Cloud (1954) thinks is now in slightly deeper water than the equilibrium depth because of a sea level rise starting about 100 yrs ago. According to this idea the reef may be experiencing a net growth of calcareous matter. However, there is no definite evidence from this study to indicate that the

reef is not in balance with respect to organic matter. Organic deposition and calcareous deposition are not necessarily in phase.

Similarly, as discussed in the section on production measurements, a balance between gains and losses may have existed on Sargent & Austin's reef also. The biggest uncertainty in both these studies is still the question of changes in dissolved organic matter in the vast flow of water crossing the reef.

We may tentatively conclude, at least, that the Japtan reef is a true climax community, in the ecological sense, under present ocean level conditions, since there is little if any net increase in living biomass.

EFFICIENCY

From tables of insolation reaching the ground (Kennedy 1949) a figure for insolation reaching the water surface can be obtained, taking into account approximate cloudiness. About $\frac{1}{2}$ of this total insolation is in the visible range (Sverdrup, *et al.* 1946). With a Weston photographic light meter enclosed in a plastic bag a reading above the surface of 1500 fc was obtained compared to 800 fc 50 cm below the surface at quadrat D. Therefore about half of the surface light reaches the average reef depth of 2 ft. From these approximations the energy available to production on the reef can be estimated. For the latitude of Eniwetok in August, these approximations indicate about 1650 KCal/m²/day incoming energy reaching the community. Relative to the 96 KCal/m²/day (24 gm x 4.0 KCal/gm) primary production estimated from oxygen measurements in Table 16 this is about 5.8% efficiency of primary production.

That this efficiency is a low one in comparison to some laboratory experiments (Rabinowitch 1951) and yet higher than average terrestrial agriculture is an important result. Here is an ecosystem which has had millions of years to evolve an effective composition, which is built for a low efficiency. This may be support for the hypothesis (Odum & Pinkerton 1955) that there is an optimum but relatively low efficiency that produces the most effective trophic structure whose survival is based on a high primary productivity.

RELATIONSHIP BETWEEN TROPHIC STRUCTURE AND COMMUNITY METABOLISM

It seems clear that the vast coral reef community is highly productive and not far from a steady state balance of growth and decay. As a community of unquestionable durability and ancient origin, it may be postulated that some kind of optimum adjustment has been evolved. The evolution may be stated in terms of the stability principle (Holmes 1948) as follows: As an open system, the construction of self regulating interactions has led by selective process to the survival of the stable.

In the previous sections a standing crop of living biomass of about 700 gm/m² was found and a total primary productivity (glucose) of 24 gm/m²/day or

8760 gm/m²/yr. The ratio of annual primary production to standing crop is therefore about 12.5 to 1. This ratio can be called the turnover. If there is an underlying relationship of primary production and standing crop under steady-state conditions, an annual turnover value similar to the 12.5 for our reef may be found in other systems where there are similar temperatures, and similar supplementary energies supplied as water currents, and similar sized organisms with similar metabolic rates.

SUMMARY

1. During a mid-summer 6-week period (1954), (1) the standing crop biomass of "producer" and "consumer" organisms of a windward, inter-island coral reef on Eniwetok Atoll was estimated, (2) primary production and total respiration were determined by upstream and downstream chemical measurements, and (3) from these data the turnover and energetic efficiency of the reef ecosystem were calculated.

2. The reef, which has not as yet been directly disturbed by nuclear explosions, exhibited 6 distinct zones as follows: windward buttress zone, coral-algal ridge, encrusting zone, zone of smaller heads, zone of larger heads, zone of sand and shingle (Figs. 2-4). Zonation of this inter-island reef (with its one-direction current system) is very different from zonation on island reefs so abundantly described in the literature. Quadrats were mapped in 5 of the zones (Fig. 5) and standing crop biomass determined for each.

3. Because producers (algae) are so intimately interwoven with animal and dead skeletal material the chlorophyll extraction method appeared to be the most feasible means of estimating producer biomass. Algal dry weight was determined by relating spectrophotometrically, chlorophyll content with known dry weights of a reference species, *Codium edule*. Various methods were used to estimate major animal components as described in appropriate sections of the paper.

4. On a horizontal surface area basis, the average living coral colony proved to contain three times as much plant as animal tissue, or .063 gm/cm² dry weight of algae as compared with .021 gm of animal polyp (Table 4 & Fig. 6). Zooxanthellae (in the coelenterate polyps) comprised only about 6% of the total plant portion, filamentous green algae embedded in the skeleton making up the bulk of plant material. The evidence indicates that these skeletal algae, often considered "parasitic" or "boring" by previous workers, may be actually mutualistic. The algal-coelenterate complex, therefore, comprises a highly integrated ecological unit (comparable to the algal-fungal complex of a lichen) which permits cyclic use and reuse of food and nutrients necessary for vigorous coral growth in tropical "desert" waters having a very low plankton content. The coral is thus conceived to be almost a whole ecological unit in itself with producer, herbivore (utilizing food from symbiotic algae), and carnivore (plankton feeding at night) aspects.

5. The quantitative coverage of coral (50-16%)

and surface encrusting algae decreased while the amount of subsurface algae increased from front to back across the reef correlated with mean current velocities suggesting a transition from a water filtering source of nutrients up front to a subsurface decomposition source of plant requirements on the back zones.

6. Although species differences were indicated, the algal content of 33 samples of 12 species of corals was rather uniform when calculated as dry biomass on a projected horizontal surface area basis (Table 5). Branching corals contained about the same amount of algae as massive and encrusting corals. Exposed reef surfaces, "deadheads," and shingle contained comparable or somewhat larger amounts of producer tissue; only the calcareous sands of the back reef gave low values.

7. While the kinds of primary producers were quite variable from place to place and zone to zone (10 major types are listed in the ecological classification), the reef, whether covered with coral or not, proved to have a rather uniform content of algae. In other words, the algal standing crop was of a similar order of magnitude (between 0.050 and 0.1 gm/cm²) throughout, a situation certainly not evident on superficial examination (because a large amount of the green plant material is subsurface).

8. The sessile part of the community is primarily autotrophic with relatively few plankton feeders other than coral polyps; fouling on glass slides was almost entirely algal.

9. In all zones of the reef a trophic structure with a pyramid of biomass was found (Fig. 10). Although entirely different taxonomic components were present in different zones, similar biomass figures were obtained. The mean standing crop for the reef as a whole in gm/m² was: producers, 703; herbivores, 132; and carnivores, 11. The ratio between standing-crop trophic levels was H/P, 18.9%, and C/H, 8.3%.

10. A very high total production of about 74,000 lbs/acre/year was obtained with the flow rate method. This represents a turnover (the ratio of annual primary production to average standing crop) of about 12.5 times per year of existing biomass. The figures and the production curve (Fig. 12) provide quantitative criteria for assaying the future effect of nuclear explosions, continued low-level radioactivity, or other factors on the community as a whole.

11. The production on the reef seems to about balance the respiration on the reef (Table 17). The corals do not constitute a dominant part of the whole metabolism. It is concluded that the reef community is, under present ocean levels, a true ecological climax or open steady-state system.

12. The efficiency of primary production computed in terms of the visible light reaching the underwater community is about 6%. This is support for the advocated theory that steady state communities adjust to a moderately low efficiency as a necessary compensation for high total productivity.

13. The reef does not derive a net gain from the

larger components of plankton in the water crossing the reef under the stress of the trade winds. Whether a dissolved organic-matter gain is obtained is still uncertain.

14. Individual corals *in situ* in nature, like those in laboratory experiments of other workers, produce an excess of oxygen in the daytime but not over the course of 24 hours (Table 16). The coral with its 3:1 ratio of plants to animals is apparently just about "balanced" in gaseous exchange.

15. The location of the sub-surface boring algae leads to a time lag in gas diffusion with the water crossing the reef and an afternoon community-production maximum (Fig. 12).

16. The nutrient levels of nitrogen and phosphorus are very low (Table 14). Some evidence exists that nitrogen is more scarce relative to plant needs than is phosphorus and must be conserved, fixed, and recirculated.

17. Measurements of low-level radioactivity which was present (Table 13, Fig. 11) provided further evidence of nutrient conservation, and autoradiograms of corals (Fig. 9) provided additional evidence for symbiosis between corals and their skeletal algae.

18. Plankton and eroded sand broken from the front-reef breaker zone is recaptured on the middle-reef zones.

19. Estimates indicate 1.6 cm of calcareous deposition per year but there is no evidence that this is not eroded almost equally rapidly.

20. The Japtan inter-island reef at Eniwetok is primarily a coral reef rather than a calcareous algal reef in the geological reef-forming sense. But like other communities studied (whether aquatic or terrestrial), the Japtan reef has a large predominance of living plant biomass, even though organisms classified as animals are more conspicuous.

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